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THE FUNCTION AND SIGNIFICANCE OF INTER-SPECIES ACOUSTIC CUES IN THE TRANSFORMATION OF BUDGERIGAR (*MELOPSITTACUS UNDULATUS*) SOUNDS INTO “SPEECH”

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ABSTRACT: Analysis of speech-imitation sounds produced by pet budgerigars (*Melopsittacus undulatus*) reveals a consistent focus on acoustic components of speech which have counterparts in the species-specific vocalizations of budgerigars. These budgerigar vocalizations include whistle sequences (which, with their rapid glides in pitch contour, need only slight modification to constitute a second-formant representation of speech), the contact call (which is acoustically similar to the second-formant transition of high front vowels), and sounds with harmonic spectra (which can be modified to represent the formant structure of certain vowels). This transformation of species-specific sounds into speech-imitation sounds by focusing on shared acoustic features prompts the hypothesis that, with the appropriate social stimulation, pet budgerigars perceive human speech as modified budgerigar sounds. The hypothesis is supported by the fact that the shared acoustic features are particularly important cues in the perception of species-specific communication sounds by both humans and budgerigars. Such inter-species vocal communication cues, having a common origin somewhere in vertebrate phylogeny, would help to explain the many reported examples of human-like speech perception by nonhuman vertebrates. The shared neural mechanisms which correspond to these shared acoustic patterns could constitute a phylogenetically conservative level of auditory perception which is communication-sound-specific but not species-specific.

INTRODUCTION

Some birds, when kept as pets, copy the communication sounds (i.e. speech) of their human companions. Although it has been valued as an entertaining curiosity for thousands of years, this remarkable behaviour has received relatively little scientific attention. Such attention is warranted, however, because copies of speech sounds by birds, when subjected to acoustic analysis, open new perspectives on

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avian vocal communication. Avian "speech" (by which term I refer both to speech-copying behaviour and to its acoustic manifestations) represents human speech after it has been filtered through an avian perceptual system, incorporated into an avian behaviour pattern, and reproduced by means of an avian vocal mechanism. It can thus provide a unique vantage point for the study of those perceptual, behavioural and vocal mechanisms.

Also, by presenting us with sounds which we perceive as "speech" but which differ, physically, from speech in a variety of ways, it can provide insight into aspects of our own communication sounds which are inaccessible to the self-scrutiny of conventional linguistics and phonetics. Finally, in demonstrating that congruent vocal mechanisms are not necessary for acoustic communication between two individuals, it emphasises the predominance of auditory over articulatory factors in vocal communication generally.

This paper will argue, on the basis of acoustic data and behavioural observations, that speech-trained, pet budgerigars (*Melopsittacus undulatus*) perceive speech sounds as modifications of species-specific budgerigar sounds, and are able to copy those "modifications" in communicative behaviour directed towards their human companions. This behaviour is facilitated principally by three factors: communicatively significant acoustic similarities between budgerigar sounds and speech (explained below); the budgerigar's adoption of those similar - albeit "modified" - communication sounds because of social bonding with a human being; the budgerigar's ability to continue modifying its communication sounds throughout life (Farabaugh *et al.*, 1994; Brittan-Powell *et al.*, 1997) to match those of its social companions.

The behavioural and acoustic evidence that birds perceive non-species-specific communication sounds (e.g. those of human speech) as if they were species-specific suggests that the former are being processed by neural pathways normally dedicated to the perception of the latter. This could be facilitated by acoustic patterns and corresponding neural mechanisms which are common to the vocal communication systems of birds and humans.

The published literature has established a rigidly dichotomous perceptual model according to which, at any particular point along the human auditory pathway, neural processing of speech is either "acoustic" or "phonetic". Within the framework of this model, human-like processing of some speech sounds by nonhuman animals is adduced as evidence that aspects of speech perception previously thought to be "phonetic" must, in fact, be "acoustic". This paper is based on analyses of budgerigar "speech" which suggest that the birds

perceive certain acoustic features of speech as being functionally identical to acoustically similar features of budgerigar sounds. It hypothesises an intermediate level of analysis which is communication-sound-specific but not species-specific. Further testing of the hypothesis could help us to escape between the horns of the dilemma posed by the artificial "acoustic-phonetic" dichotomy. It could also lead to new insights into the evolution of vocal communication - including human speech.

The aims of the paper are thus to present some unprecedented observations of budgerigar "speech", to propose an explanatory hypothesis and to show how that hypothesis relates to current knowledge and theory. In pursuing the last-mentioned aim, the remaining Introduction selectively draws on the extensive literature relating to avian vocal communication and the Discussion draws on the even more extensive speech-perception literature. While neither section is intended as an exhaustive review, some detailed discussion of this literature was considered necessary.

Acoustic similarities

Bertram (1970) and Nottebohm (1976) drew attention to acoustic similarities between human speech sounds and certain species-specific vocalizations of the Indian hill mynah (*Gracula religiosa*) and the orange-winged Amazon parrot (*Amazona amazonica*) respectively. Each author associated these similarities with the ability of his subject species to imitate speech sounds. In both cases, the speech-like species-specific vocalizations are used in "close-range social contact" (Bertram, 1970), and their acoustic structure resembles that of human vowels in their low-frequency periodicity and apparent formant structure.

Some calls and song syllables in the complex vocal repertoire of the budgerigar display these and other speech-like features. The budgerigar repertoire consists of at least 11 (and possibly as many as 14) call types (Higgins, 1999, p. 515) as well as the complex and variable vocal pattern known as "warble" (Brockway, 1964, who distinguished between "loud warble" and "soft warble") or "warble song" (Farabaugh *et al.*, 1992). The latter term is used here, as it emphasises the important fact that this vocal pattern is in some respects analogous to passerine song. Indeed, Ferrell and Baptista (1982) maintain that budgerigar warbling is "functionally equivalent" to passerine song. Warble song consists of call notes as well as song-specific syllables (Wyndham, 1980; Farabaugh *et al.*, 1992; Brittan-Powell *et al.*, 1997), providing psittacine support for the theory that bird song evolved from calls (Thorpe, 1958; Thielcke, 1966; Catchpole, 1979).

Brockway (1964) described "loud warble" as "the chatter so commonly associated with this species". The use of the word "chatter" suggests the speech-like quality of budgerigar warble song, and the spectrograms of Farabaugh *et al.* (1992) and Wyndham (1980) confirm this similarity. Some warble song syllables are broad-bandwidth sounds with formant-like concentrations of energy - particularly in the region of human second-formant frequencies (about 800-2,500 Hz).

Behavioural parallels between warble song and speech imitation

Brockway (1964), Farabaugh *et al.* (1992) and Wyndham (1980) all remark on the highly variable nature of warble song. In spite of its wide range of syllable types and the high variability of its sequencing, Farabaugh *et al.* (1992) detected the possible existence of combinatorial rules and therefore of a learnt "syntax" in the structure of warble song.

Warble song is primarily a courtship vocalization (Brockway, 1964; Wyndham, 1980; Farabaugh *et al.*, 1992), but can be used in other forms of social interaction (Farabaugh *et al.*, 1992). Wyndham's (1980) observations, and the studies of Farabaugh *et al.* (1992, 1994), indicate that warble song contains cues for individual (and group) identification. Warble song is most commonly performed by males, but can also be performed by females (Ferrell and Baptista, 1982). Its performance is highly "mimetic" (Brockway, 1964; Ferrell and Baptista, 1982): one budgerigar is stimulated to warble by hearing another. However, a warbling performance is not obviously directed at any other individual (Brockway, 1969).

Vocal imitation plays an important role in warble song acquisition and modification, with social factors influencing the pattern of imitative learning. Farabaugh *et al.* (1992) found that males in the same social group shared a significantly greater percentage of syllable types than males in different social groups. The contact call, which is one of the most common components of warble song, is both learnt from adults and matched among siblings. Even if the adult model is aberrant (due to deafening) or of another species (e.g. zebra finch, *Taeniopygia guttata*), its influence is evident in the contact calls of juvenile budgerigars (Brittan-Powell *et al.*, 1997).

These characteristics of the budgerigar's warble song have their parallels in the "verbal" (i.e., speech-imitation) behaviour of the birds. Male budgerigars are recognised by fanciers as the best "talkers", but females are capable of imitating speech. Verbal behaviour in this species is usually stimulated by human chatter or noise in the environment; thus it is "mimetic" in Brockway's sense, as well as being

imitative in its use of vocal copying. The budgerigars recorded during the present study showed, when "talking", no interactive orientation towards any human companion; their verbal utterances were seldom in direct response to utterances of a human speaker.

In contrast to the verbal behaviour of budgerigars, that of some other "talking" species, such as some larger parrots and the Indian hill mynah, is often an overt interaction with human companions. Whereas the budgerigar, once in the necessary psycho-physical state of arousal, tends to run right through the verbal repertoire in a fixed order, these other species are more inclined to produce particular verbal utterances as a direct and specific response to verbal or other environmental stimuli. I have argued [Scanlan, 1988] that this behavioural distinction reflects the modelling of budgerigar "speech" on *singing* behaviour, in contrast to the modelling of mynah "speech", or that of the larger parrots, on *calling* behaviour.

The following three sections discuss the ontogeny and neuroethology of learnt avian vocalizations with relation to budgerigar "speech" and human speech. For a review of the literature relating to ontogenetic and neuroethological correspondences between human speech and oscine song, see Doupe and Kuhl (1999).

The development of avian "speech": ontogeny of song in birds parallels that of speech in humans

The two *Melopsittacus undulatus* subjects of this study had been carefully trained by their owners to repeat a fixed repertoire of phrases and verses. Both these birds, before entering upon their repertoires, would go through a preparatory performance which began as species-specific warble song and included an ever-increasing number of speech-like sounds until the repertoire itself was begun. This sequence, which I have called "pre-performance warble" (Scanlan, 1988), contains speech phrases and syllables which are not part of the performance repertoire. This conforms with the eclectic nature of warble song as described by Brockway (1964), Wyndham (1980), and Farabaugh *et al.* (1992). It also suggests a possible connection with the plastic song of songbirds, which includes a wide variety of vocalizations and, in some cases, imitations of other species. (See Thorpe, 1955, and Marler, 1956, although these early studies had not yet distinguished between "plastic song" and the ontogenetically earlier "subsong".) Physically, oscine plastic song as presented in the literature has a broader - and therefore more speech-like - spectral envelope than full song. (See spectrograms in, for example, Thorpe and Pilcher, 1958, and Marler and Peters, 1982.) Like warble song and speech imitation in budgerigars, it is

mainly performed by males, but can be performed by females.

The "pre-performance" or speech-like warble of pet budgerigars has its parallels in the vocal behaviour of other "talking" species. Groups of captive Indian hill mynahs (Foss, 1964) and European starlings, *Sturnus vulgaris* (West *et al.*, 1983), exposed daily to the speech of their human carers, developed vocal timbres and cadences which resembled those of speech.

Many authors, including Charles Darwin in *The Descent of Man* (1871), have compared subsong and plastic song in songbirds with babbling in human infants. (See, e.g., Thorpe, 1961; Kuhl, 1989; Locke, 1993.) Menyuk and Menn (1979), in discussing the babbling of infants, describe the boundary between babble and speech as "in general a fuzzy one". At this stage in the child's development, they say, there are "recurrent entities" in a child's production that cannot be classified unequivocally as either "babble" or "speech". In some children these entities "occupy a pivotal position in language development, and careful consideration of their form and function illuminates the nature of the transition from babble to speech in the general case" (Menyuk and Menn, *ibid.*). This paper examines some analogous "entities" in the pre-performance warble of "talking" budgerigars. These "entities" are, in their acoustic structure, transitional between species-specific sounds and speech-imitation sounds. In this, as well as in their loose overall organization and their preparatory, exploratory function, they resemble avian plastic song. Thus they provide clues to the motivation and the mechanisms involved in the transformation of budgerigar sounds into "speech". (The word "transformation" in this paper refers both to modifications of acoustic structure, and to the - much more dramatic - change in the corresponding aural impression.)

Social and sequential factors involved in avian vocal learning

At least some songbirds - e.g. zebra finches (Slater *et al.*, 1988) and white-crowned sparrows, *Zonotrichia leucophrys* (Marler, 1970) - appear to be genetically predisposed to learn species-specific song, but cross-fostering experiments with both finches (Immelmann, 1969; Eales, 1987, 1989) and white-crowned sparrows (Baptista and Petrinovich, 1984, 1986) have demonstrated that any such predisposition can be overridden by social factors. Furthermore, in laboratory finches, social interaction - visual as well as vocal - between tutor and pupil is necessary for song learning to occur with a precision comparable to that observed in the wild (Eales, 1989).

Although, in captivity, some birds can learn species-specific song from tape recordings (Marler and Tamura, 1964; Adret, 1993), the

learning of *species-specific* calls and songs by a bird typically involves a familial (e.g. Clayton, 1987), social (e.g. Payne, 1981) or antagonistic (e.g. Baptista and Petrinovich, 1984) relationship with the model/tutor. In the earlier study on which this paper is based (Scanlan, 1988), it was argued that learning of *non-species-specific* vocalizations by birds is of two distinct kinds - that in which there is such a relationship with the model, and that in which there is no such relationship. In the former case, the overall behaviour pattern (including ontogeny, neurophysiology, and social context) is exactly the same as that in the learning of species-specific sounds and should thus be referred to by the same term ("vocal imitation"). The term "vocal mimicry", then, should be restricted to those instances of non-species-specific vocal copying in which no familial/social/antagonistic relationship is involved (and in which, as a corollary, ontogenetic and neurophysiological patterns differ from those associated with "imitation"). The argument of this paper involves classifying speech imitation by budgerigars as "vocal imitation".

Social factors determine the species-specific call-learning behaviour of budgerigars. Farabaugh *et al.* (1994) found that the contact calls of unrelated budgerigars converged on a common acoustic pattern soon after they had been confined together in the same cage. (Nowicki, 1989, reported a similar result with the flock-recognition call of the black-capped chickadee, *Parus atricapillus*.) Evidence presented below will demonstrate that modification of the contact call is an important ingredient in the process of a budgerigar's transforming species-specific sounds into "speech".

Early experiments on song learning in captive birds (e.g. white-crowned sparrows - Marler, 1970, and zebra finches - Immelmann, 1969) established the concept of a "sensitive period", after which normal learning could not occur. However, further experimental work with both these species (white-crowned sparrows - Baptista and Petrinovich, 1984, 1986; zebra finches - Eales, 1985, 1987) made it clear that the sensitive period was not immutable, but could be extended if a suitable model had not been found by the end of the usual song-learning period.

There is a growing body of evidence that, in the wild, vocal learning in some birds is open-ended - i.e., it is not restricted to a sensitive period early in life. (See reviews in Mundinger, 1982; Farabaugh *et al.*, 1994; Doupe and Kuhl, 1999. The learning of novel vocalizations should be distinguished from the process of selective matching with an early-acquired set of models revealed, for example, in the white-crowned sparrow by Nelson and Marler, 1994.) In terms of the traditional distinction between calls and song (Thorpe, 1958;

Thielcke, 1966; Nottebohm, 1972), open-ended learning strategies seem to apply particularly to call learning (Farabaugh *et al.*, 1994). However, modification of song in adulthood has been documented in several species - e.g. in the canary, *Serinus canarius* (Nottebohm and Nottebohm, 1978), and especially in species in which song has an important social as well as sexual/territorial function, such as the European starling, (Adret-Hausberger *et al.*, 1990; Chaiken *et al.*, 1994; Mountjoy and Lemon, 1995), the Australian magpie, *Gymnorhina tibicen* (Brown *et al.*, 1988), and the Indian hill mynah (Bertram, 1970). Even in species - such as the zebra finch - in which song learning normally occurs during a clearly-defined period (Immelmann, 1969), learning can be delayed indefinitely in captivity if no suitable model is available during the usual sensitive period (Eales, 1985).

Farabaugh *et al.* (1994) showed that the learning and modification of budgerigar contact calls is an open-ended process. An earlier study (Farabaugh *et al.*, 1992) had shown that contact calls - and other calls - are important components of budgerigar warble song. To this extent at least, then, warble song is subject to learnt modification throughout adulthood. The extent of such modification to the highly variable overall structure - both acoustic and syntactic - of budgerigar warble song is as yet unknown. It will be argued below, however, on the basis of acoustic analyses presented here, that speech imitation is a learnt modification of warble song. Budgerigar "speech" would thus demonstrate this species' ability to modify its song extensively and open-endedly in adjusting to a novel social environment.

In songbirds that modify their song repertoires as adults there is evidence that plastic song occurs in adulthood (reviewed in Margoliash *et al.*, 1991), suggesting a connection between plastic song and not only song learning in juveniles but also song modification in adults (Marler and Peters, 1982; Margoliash *et al.*, 1991). European starlings have a "warbling song" (Adret-Hausberger and Jenkins, 1988) which appears to be analogous to budgerigar warble song in both structure and function. Hausberger *et al.* (1991) remarked on the plastic-song-like nature of the starling warble song; the same could be said of the warble song of budgerigars. It will be shown below that every time a budgerigar performs a speech-imitation sequence it does so by modifying some of its species-specific sounds. The association of each "speech" sequence with a sequence of "pre-performance warble" thus emphasises the analogy between "pre-performance warble" in speech-trained budgerigars and plastic song in songbirds. Considered as a whole, a bout of pre-performance warble by a pet budgerigar, which becomes increasingly more speech-like throughout, seems to reproduce, in a condensed form, the "speech"-learning process in the bird.

Neuroethological factors

Patterns of neural activity are fundamental ingredients of the behaviour patterns observed by ethologists. The integrated study of ethological and neural events has developed into the discipline of "neuroethology" (see, e.g., Suga, 1988; Brenowitz and Kroodsma, 1996). Over the past 20 years, researchers have uncovered neural activity patterns which form an integral part of audio-vocal communication behaviour in birds. In songbirds, some of these patterns are associated with neural pathways reserved for the process and/or the product of vocal learning. These pathways include feedback circuits from auditory to vocal telencephalic centres (Kelley and Nottebohm, 1979; Doupe and Konishi, 1991), pathways devoted to the production of learnt song components as distinct from unlearnt components (Simpson and Vicario, 1990), and an "anterior forebrain pathway" apparently crucial to the process of vocal learning (Bottjer *et al.*, 1984, 1985; Doupe and Konishi, 1991; Herrmann and Arnold, 1991; Mooney and Doupe, 1991; Scharff and Nottebohm, 1991; Doupe, 1997). The vocal control nuclei along these pathways contain auditory units which are maximally responsive to autogenous (i.e., the bird's own) song (Margoliash, 1983, 1986; Margoliash and Fortune, 1992; Vicario and Yohay, 1993; Doupe, 1997; Whaling *et al.*, 1997). This selectivity applies even if autogenous song is abnormal as a result of experimentally manipulated learning (Margoliash, 1983). Thus, in the learning and production of non-species-specific sounds, if environmental, social and metabolic aspects of the behaviour pattern are preserved, neural aspects of the pattern may also be preserved.

Physical similarities between the vocalizations of some avian species and human speech could facilitate this process. For example, Chew *et al.* (1996) found neurons in the caudomedial neostriatum of the zebra finch which respond strongly to human speech sounds as well as to species-specific calls. These neurons respond less strongly to the calls of other, related, songbird species. In this case, the strength of the response appears to be directly related to acoustic similarities between zebra finch calls and speech - similarities not shared by the alien bird sounds.

It can be hypothesized, therefore, that a "talking" songbird (e.g. a speech-trained Indian hill mynah) employs its specialised vocal-communication neural pathways in the perception of speech and the production of speech-like sounds and that consequently, in the vocal control nuclei of such a bird, there would be units maximally responsive to its own speech-imitation sounds.

Parrots differ from songbirds not only in the organization of

telencephalic vocal control centres, but also in the systems of projections from auditory to vocal centres (Striedter, 1994). The one parrot species examined so far - *Melopsittacus undulatus* - has three recurrent vocal-control pathways in the anterior forebrain (Durand *et al.*, 1997). These pathways may be, anatomically, either analogous to (Brauth *et al.*, 1994) or homologous with (Durand *et al.*, 1997) the anterior forebrain pathway in songbirds; in either case, the corresponding role of vocal learning in songbird and budgerigar ontogeny reinforces the conclusion that in budgerigars, too, they have a vocal-learning function (Brauth *et al.*, 1994; Durand *et al.*, 1997). Indeed, their greater neurological complexity in the budgerigar could reflect that species' greater flexibility in the acquisition of new vocalizations (Durand *et al.*, 1997). Preliminary reports indicate that Anna's hummingbird (*Calypte anna*) which, like at least some other hummingbirds (Gaunt *et al.*, 1994), develops its song through vocal learning (Baptista and Schuchmann, 1990), has forebrain nuclei similar in appearance to those of songbirds (Brenowitz and Kroodsma, 1996). Thus the hypothesis in the previous paragraph relating to songbirds may be extended to apply to budgerigars (as well as to other parrots and hummingbirds).

In summary, neurological data indicate the existence, in songbirds and budgerigars, of complex, specialised audio-vocal neural pathways for the processing of learnt communication sounds. They also indicate that these pathways can operate whether the learnt vocalizations are normal (i.e. species-specific) or abnormal (e.g. allospecific). The hypothesis explored in this paper is that there are acoustic cues, common to a range of vertebrate communication sounds, which, when experienced in conjunction with the necessary social stimuli, allow certain vocalizations - whether species-specific or allospecific - access to these special pathways. Experimental evidence for the existence of such acoustic cues is presented below.

METHODS

What follows is an analysis of several sequences from the pre-performance warble of two pet budgerigars (Budgerigar A and Budgerigar B - each trained by a different adult female owner) which illustrate the transformation of bird sounds into "speech". Each bird had been trained, over a number of years, by its owner's repeating a sequence of words and phrases (having a total duration, in each case, of 30-45 sec) in a stereotyped order and intonation pattern. In each case, too, training occurred in training sessions which were clearly defined by

time of day, the orientation of the owner in relation to the bird's cage (e.g. closer than at other times), and the distinctly pedagogical attitude of the owner during these sessions (e.g. demanding the bird's attention). Each bird was recorded in its cage in its owner's home, and each on a different day. On each of those days, the respective human trainer was recorded repeating her bird's repertoire in the manner (i.e., using the stereotyped intonation pattern) employed during training sessions.

Budgerigar A ("Lucky") was recorded with a Uher Report tape recorder, and Budgerigar B ("Joey") with a Uher CR 240 cassette recorder. The microphone used for both recordings was a Sony Electret condenser microphone, ECM-30. In both cases, the microphone was suspended from the wire forming one side of the bird's cage, and it took both budgerigars about one hour to become comfortable enough with this novel object (and the presence of the investigator) to resume normal vocalization.

Both birds began vocalization with sequences of "pre-performance warble" which led into repetitions of their repertoires; however, the distinction between pre-performance warble and performance proper was more marked in Budgerigar A than in Budgerigar B. The tape recorder was switched on near the beginning of each sequence of "pre-performance warble". Each recording session lasted about four hours: in that time, Budgerigar A produced seven clearly-defined sequences of "pre-performance warble" plus repertoire, and Budgerigar B several sequences, in each of which it was possible to distinguish an initial "pre-performance" and a subsequent "performance" component. Both owners confirmed that, despite the presence of the microphone and the investigator, the sequences were typical of the birds' vocalizations. The spectrograms were produced on a Kay Sona-Graph 6061B, using the 300 Hz bandwidth filter.

RESULTS

Harmonic spectra

A common syllable in budgerigar warble song is a strident-sounding array of harmonically related components. This sound is designated "brr" by Brockway (1964) and "weep" by Farabaugh *et al.* (1992), but in this paper I will continue to use my term "harmonic warble" (Scanlan, 1988), which is descriptive of its acoustic structure. Amplitude spectra of harmonic warble sounds confirm that their components are, indeed, harmonically related; moreover, the corresponding sound pressure waveforms, strikingly similar to those of

human vowels, indicate that the budgerigar could be using a sound-production mechanism similar to that of human phonation, as explained in my original study (Scanlan, 1988). In a non-speech-imitation context it has a fundamental frequency, producing an intense spectral peak, of 1-2 kHz (see spectrograms in Farabaugh *et al*, 1992) - i.e., the range of the second formant, rather than the fundamental, of human vowels. Within the pre-performance warble of the two budgerigars under investigation here, however, fundamental frequencies of harmonic warble varied between the 1-2 kHz typical of a non-speech-imitation context and frequencies below 1 kHz in syllables which sounded more speech-like. In other words, an initial mechanism employed by these budgerigars in transforming harmonic warble to "speech" is a simple lowering of fundamental frequency.

Figure 1, a sequence of Budgerigar B's pre-performance warble, demonstrates further stages in this transformation. This sequence shows a progression from speech-oriented, low-frequency harmonic warble to actual speech imitation in which the main factors in the transformation are the spectral and temporal qualities of the initial burst of noise, and the pitch contour of the succeeding vocalic segment. The harmonic warble syllable (labelled "1" at the top of the spectrogram) is followed by an intermediate stage (2), and then by the speech imitation proper (3). It is obvious from the spectrogram that the bird has modified 1 only minimally to produce the very different perceptual effect of 3. This, however, is not the only mechanism available to a budgerigar for the imitation of vowels: an alternative mechanism involves the amplitude modulation of a sinusoidal carrier (Scanlan, 1988; Banta Lavenex, 1999), the carrier and modulation frequencies being within the ranges of human second-formant and fundamental frequencies respectively (Scanlan, 1988).

While there is no formant pattern in 1, there are discernible spectral peaks in 2 and 3, the first vocalic segment of 3 having a "formant transition" from about 2,000 Hz to 1,000 Hz. These are frequencies appropriate for the transition from an initial palatal fricative [dʒ] to a mid vowel such as [ə]. (Compare the speech pattern of the bird's trainer in pronouncing the same sound sequence in Figure 2.) The fricative noise at the beginning of (3) has a similar frequency range (mainly between 2,000 Hz and 4,500 Hz), intensity, and duration (46 msec) to those in the same word - the bird's name, "Joey" - pronounced by his trainer (Fig. 2). The overall contour of the harmonic components has been modified in (3) to resemble the falling and then rising contour of F2 in Figure 2.

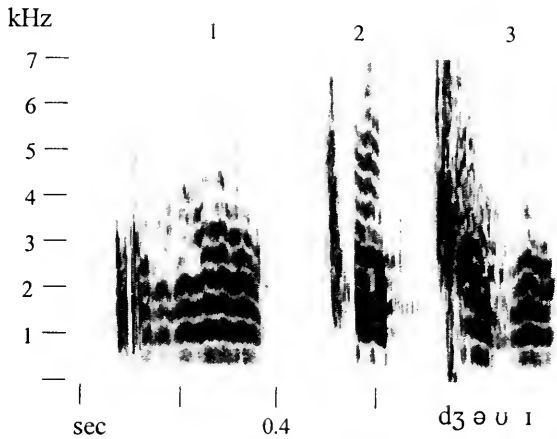


Figure 1. A sound sequence produced by Budgerigar B illustrating the transformation of a species-specific syllable (of the “harmonic warble” type - see text) into an imitation of the name Joey [dʒəʊi].

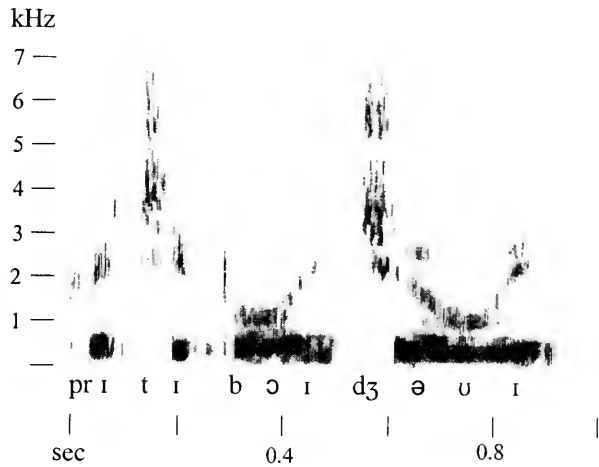


Figure 2. The phrase “pretty boy Joey” [prɪtɪ bɔɪ dʒəʊi] produced by the woman trainer of Budgerigar B, for comparison with Figure 1 [dʒəʊi], Figures 3 and 4 [prɪtɪ bɔɪ], and Figures 6 and 7 [bɔɪ].

Whistles and the second formant

Amplitude modulation is a common feature of bird sounds (Greenewalt, 1968; Stein, 1968), and the reported range of avian amplitude-modulation frequencies (90-300 Hz - Stein, *ibid.*) roughly corresponds with the range of fundamental frequencies in adult human speech (Lieberman, 1977). For human listeners, amplitude-modulation frequency is the acoustic correlate of perceived pitch (Ritsma, 1962; Schouten *et al.*, 1962).

Amplitude modulation is a dominant feature of both species-specific contact calls and speech-imitation sounds produced by budgerigars (Banta Lavenex, 1999). Budgerigars are more sensitive than humans to changes in amplitude-modulation rate (Dooling and Searcy, 1981). Furthermore, budgerigars are better able than humans to detect a tone of 2-4 kHz within a band of noise (Dooling and Saunders, 1975; Saunders *et al.*, 1979; Dooling and Searcy, 1980, 1985). This range (2-4 kHz) also represents the peak in the budgerigar's audibility curve (Dooling, 1982; Dooling and Saunders, 1975; Dooling *et al.*, 1978, 1979). These findings suggest that budgerigars may perceive some vowel sounds as a "carrier" (i.e. the peak component of F2) surrounded by "modulation-induced sidebands" (i.e. harmonic components). The hypothesized use by birds of equally-spaced spectral components in the perception of pitch is comparable to the use of harmonic spacing by human listeners in the perception of fundamental frequencies in speech (Remez and Rubin, 1984).

My acoustic analysis of budgerigar "speech" has revealed that F2 is, indeed, the acoustic axis of these vocalizations (Scanlan, 1988). It has also revealed consistent variation of modulation patterns - both AM and FM - within a budgerigar's "speech" repertoire which indicate that such patterns, which may be communicative features of species-specific vocalizations, have been imposed with communicative intent on the appropriated speech-imitation sounds. This is consistent with the finding of Lohr and Dooling (1998) that budgerigars are much more sensitive than humans to anomalies in harmonic patterns.

Sequences of whistles with patterns of rapidly changing frequency within the range of human F2 are common components of budgerigar warble song (related to the "contact", "chirly" and "widdly" calls of Farabaugh *et al.*, 1982). These whistled sequences resemble, in both frequency range and frequency modulation (Dooling *et al.*, 1995), individual components of the synthetic "sinewave speech" used in speech-perception experiments (Remez *et al.*, 1981, 1994; Best *et al.*, 1989). My study showed that, by amplitude modulating whistles such as these, a bird can create the auditory impression of low-frequency

“voicing” (Scanlan, 1988). At the pre-performance warble stage, however, patterns of amplitude modulation can still be more bird-like than voice-like, and the main adaptation towards “speech” is a matching of whistle frequency contours with the changing contours of spectral peaks - principally those representing F2 - in the speech signal.

Figure 3, taken from the pre-performance warble of Budgerigar A, shows that only minimal alterations are required to transform species-specific whistles into crude representations of speech sounds. The spectrogram represents the bird’s imitation of a phrase - “pretty pretty boy” [prɪtɪ prɪtɪ bɔɪ] - followed by a whistle sequence which bears a strong resemblance to the phrase. The plosive burst and upward “second-formant transition” of the first [prɪ] have their counterparts in the rapid release and initial upward glide of the first whistle (at 1.2 sec on the spectrogram). The plosive burst, aspiration noise, and falling second-formant transition of [tɪ] are precisely mirrored - in both frequency range and transition slope - in the rapid release and downward glide in the first whistle. The second [prɪtɪ] is a simplified version of the first. In the third word, the rising second-formant transition of [ɔɪ], at 0.8 sec, has its counterpart in an excursion of similar slope over an identical frequency range (1,200 Hz - 3,300 Hz) at the end of the final whistle. These segments bear a strong resemblance to the second-formant transition in the human-speech version of [bɔɪ] (Fig. 2). The overall timing of the whistle sequence matches that of the “speech” sequence at about 0.9 sec.

While it is remarkable that the vocalization represented by Figure 3 should be perceived by human listeners as “speech”, experiments have confirmed that synthetic speech signals consisting simply of three sinusoidal components - representing F1, F2 and F3 - are intelligible to naive listeners (Remez *et al.*, 1981), and trained listeners to “whistled speech” (Busnel and Classe, 1976) can recover the full phonetic content of a single-sinusoid representation (Busnel *et al.*, 1970). In the example presented here, the amplitude modulation of the sinusoidal F2 representation is sufficient to create an impression of “voicing”.

Figure 4 was derived from the recording of Budgerigar B, which produced the same phrase as Budgerigar A [prɪtɪ prɪtɪ bɔɪ] in pre-performance warble and, like Budgerigar A, followed the “speech” sequence by a series of whistles resembling it in both spectral and temporal dimensions. The overall sequence has a broader and lower-frequency spectrum than that of Figure 3, and in those respects is more speech-like than the earlier example. In Figure 4 the tripartite temporal structure of the whistled sequence, and its frequency contour pattern,

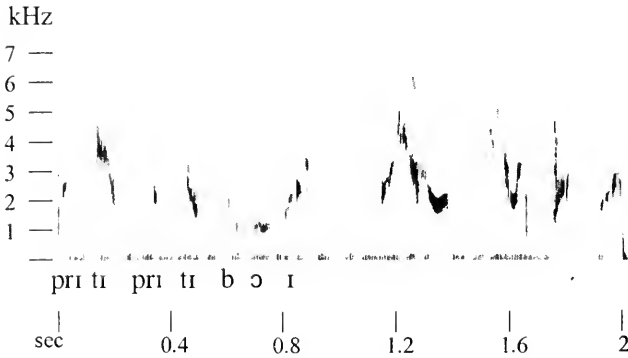


Figure 3. A sound sequence produced by Budgerigar A during “pre-performance warble”: the phrase “pretty pretty boy” [pri ti pri ti b o i] followed immediately by a series of species-specific whistles (at 1.2 - 2.0 sec) mirroring several acoustic features (see text) of the speech-imitation phrase.

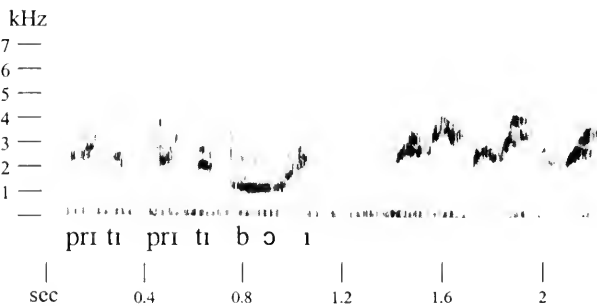


Figure 4. The same speech-imitation phrase as in Figure 3, this time produced by Budgerigar B during “pre-performance warble”. In this instance, too, an immediately-following series of species-specific whistles reproduces several spectral and temporal features (see text) of the speech-imitation phrase.

follow the "speech" sequence even more closely than their counterparts in Figure 3. In Figure 4 the rising contours associated with the high front vowels in [pɾɪ] and [bɔɪ] have particularly obvious correlates in the whistled sequence.

Experiments by Dooling *et al.* (1995) have shown that budgerigars can discriminate among three-formant synthetic /ra/ and /la/ syllables using the same cue - F3 transition - as human listeners. Furthermore, they can discriminate in a similar fashion among single-sinewave stimuli which follow the frequency modulation patterns of F3 in the /ra/-/la/ continuum. (The F3 frequency range in these stimuli was about 1,700-2,800 Hz.) These results suggest that budgerigars may hear single-sinusoid signals as speech-like if those signals incorporate cues which are sufficient for discrimination among speech sounds. The corollary, of course, is that they may reproduce speech as a single-sinusoid signal incorporating those critical cues.

The examples of Figure 3 and Figure 4 suggest that, for both birds, there is a strong association between the speech-imitation and species-specific sounds. Further analysis - some of which is presented below - demonstrates that this association is at least partly based on acoustic similarities between the high front vowels /i/ and /ɪ/ (and their transitions to adjacent speech sounds) and certain narrow-bandwidth elements of budgerigar warble song.

The contact call and high front vowels

Perhaps the most convincing evidence for the transformation of a natural sound pattern into an imitation of speech is to be found in those sequences in which speech-like sounds have replaced only part of the original species-specific pattern or, conversely, in which a species-specific element has been reintroduced into an imitated word or phrase. In the pre-performance warble of budgerigars, this is most common in the case of the high front vowels /i/ and /ɪ/, which share some important acoustic characteristics with the most common call of the budgerigar, the contact call (Park and Dooling, 1985; Farabaugh *et al.*, 1992, 1994, 1998; Farabaugh and Dooling, 1996; Brittam-Powell *et al.*, 1997). These vowels, like the contact call, have a strong concentration of energy (high F2 + F3) at about 2,000-3,500 Hz. The contact call is also characterised by rapid glides which, in speech imitation, can be adapted to serve as transitions to a high second formant. Indeed the second-formant transitions of normal human speech, if isolated, sound so like bird vocalizations such as budgerigar contact calls (labelled "chprs" by Wyndham, 1980) that they are called "chirps" in the literature of

phonetics (Mattingly *et al.*, 1971).

The finding of Farabaugh *et al.* (1998) that the spectral structure of contact calls in wild and domesticated budgerigars is essentially the same, emphasises the typical, species-specific nature of the pet budgerigar's "chrp". Domesticated budgerigars are able, however, to discriminate among contact calls which have been experimentally highly distorted (Park and Dooling, 1986).

Figure 5 shows a sequence of pre-performance warble by Budgerigar A in which a contact-call-like vocalization (subsequently referred to as a "chrp") has taken the place of the [ɪ] sound in the speech-imitation phrase "clever boy" [klevə bɔɪ]. Comparison of this sequence of pre-performance warble, having a mixture of speech-like and avian elements, with a completely "spoken" version (Fig. 6), produced by the same budgerigar (Budgerigar A) during a full performance, demonstrates the similarity between the rapid upward glide at the beginning of the "chrp" and the second-formant transition from [ɔ] to [ɪ] in the word [bɔɪ]. The energy in the [ɪ] sound in the "spoken" phrase is centred on about 2,800 Hz, as is that in the "chrp".

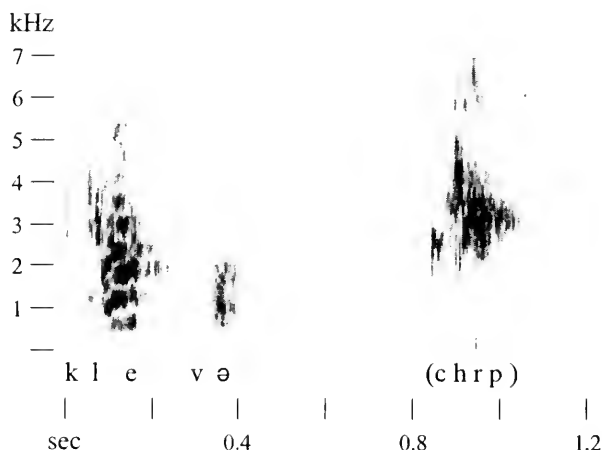


Figure 5. Budgerigar A, in a bout of "pre-performance warble", begins to produce the phrase "clever boy" [klevə bɔɪ], which forms part of his speech-imitation repertoire, but substitutes for the word [bɔɪ] a species-specific contact call. This call is acoustically similar to the vowel [ɪ] which ends the word [bɔɪ]. In timing, the contact call occurs precisely when the [ɪ] sound of the complete phrase (see Figure 6) is due.

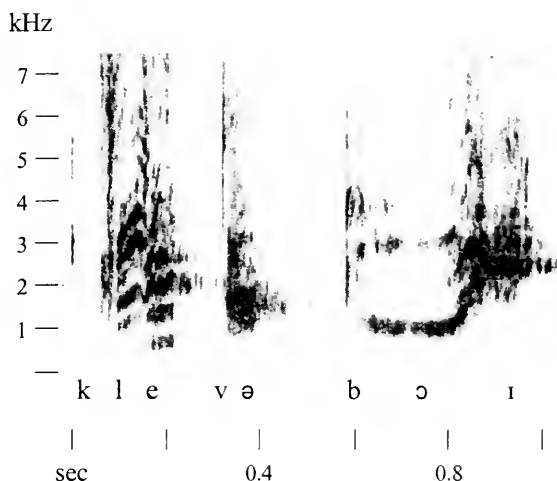


Figure 6. The phrase “clever boy” [klevə bɔɪ] from a full performance of Budgerigar A’s repertoire, for comparison with the “pre-performance warble” version of the phrase in Figure 5, and of the word [bɔɪ] in Figures 3, 4 and 7.

Compare Figure 6 with the human-voice version of [bɔɪ] in Figure 2, and note the similarity of the F2 transition patterns.

Further evidence that the “chrp” in Figure 5 represents the final section of the word [bɔɪ] is the presence on the original spectrogram (although not clearly visible on its reproduction here) of a click, like the plosive burst of [b], about 0.13 sec before the onset of the “chrp”. Relative timing is also an important clue: the onset of the “chrp” in Figure 5 occurs 0.83 sec after the initial plosive burst in [klev-], and exactly the same interval separates the beginning of the [ɪ] sound in Figure 6 from the beginning of the phrase. The durations of the [ɪ] sound and the “chrp” are similar.

Figure 7, another sequence from the pre-performance warble of Budgerigar A, shows the word [bɔɪ] followed immediately by a “chrp” which retains many of the acoustic features of the [ɔɪ] sound. The main area of intensity is within the same frequency range (2,000-3,500 Hz, the F2-F3 region of high front vowels) and the contour of the second-formant transition in [ɔɪ] resembles, albeit in a lower frequency range, the steep upward glide of the “chrp”. As in the whistle sequences, this juxtaposition of acoustically similar species-specific and speech-like sounds suggests that this similarity has significance for the bird.

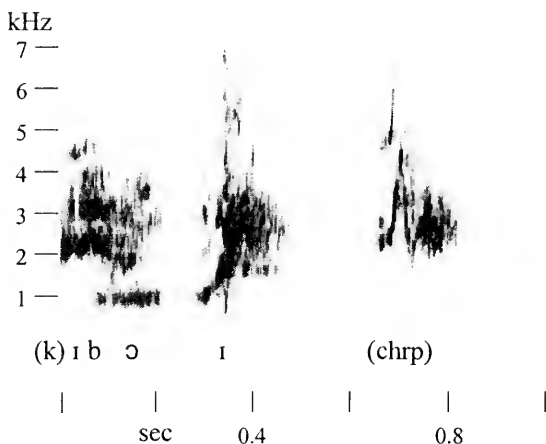


Figure 7. A sequence of "pre-performance warble" from Budgerigar A in which part of the phrase "Lucky boy" [(lɜk)ɪ bɔɪ] is followed immediately by a species-specific contact call which is acoustically similar to the [ɔɪ] section of [bɔɪ].

DISCUSSION

The analysis above has identified components of budgerigar and human communication sounds which are similar in acoustic structure. It indicates that, in copying speech, budgerigars focus on components of the speech signal which resemble components of budgerigar warble. These "shared" components (e.g. the frequency modulations typical of budgerigar contact calls and human second-formant transitions) are of particular communicative significance in both human and budgerigar vocalizations. Suga (1988) has suggested that if animals and humans produce similar acoustic patterns, they could share similar neural mechanisms for perceiving them. The corollary to Suga's hypothesis is that, under the right circumstances, a neural mechanism designed for "special" perceptual processing of a species-specific vocal pattern could afford such "special" processing to an acoustically similar non-species-specific vocalization. The data presented here support this view: the incorporation of speech sounds into the budgerigar's communicative

repertoire indicates that these non-species-specific sounds are being processed by such "special" perceptual mechanisms. (The perception of a sound as being an appropriate model for imitation is an essential ingredient of the overall perceptual-motor pattern of vocal learning. Extrapolation from observed vocal production to inferred auditory perception is thus a valid procedure.) This perceptual phenomenon could help to explain the human-like results of speech-perception experiments using avian (and other non-human) subjects.

Levels of analysis

One of the basic concerns of speech perception research has been to investigate the progressive analysis of the speech signal as it ascends from the periphery. The tendency has been to attempt to isolate discrete "levels" of analysis, the most commonly-drawn distinction being that between an "acoustic" or "auditory" level and a "phonetic" level (e.g. Pisoni, 1973). The experimental results of Cutting (1976) and Samuel and Kat (1996) even prompted those authors to propose the existence of several "auditory" levels at progressively higher stages of abstraction and integration. It has been axiomatic in the literature that, when a non-human animal successfully discriminates among speech sounds according to human-like categories, the categorisation occurs at an "auditory" level of perception because, by definition, it cannot happen at a "phonetic" (i.e., speech-specific) level (Kuhl, 1981, 1988; for a more recent review see Fitch *et al.*, 1997). Such animal results have been regarded, by analogy, as evidence that the speech-sound discriminations in question must rely on "auditory" processes in human listeners as well (Kuhl, 1987).

The term "levels of analysis" as used in the phonetics literature can be confusing: it seems to imply an anatomical correlate to what is usually no more than a simple conceptual scheme imposed on a highly complex neurological process. While there are undoubtedly hierarchical patterns within this process, references to "levels of analysis" in the present paper should *not* be understood as referring to anatomically identifiable centres along the neural pathway for the perception and recognition of communication sounds.

This paper argues, on the basis of the data presented above, that in humans and at least some other vertebrates speech sounds pass through a level (or levels) of perceptual analysis which is neither simply auditory nor specifically phonetic, but which is specially designed to process the complex acoustic cues which are common and peculiar to the communication sounds of many vertebrate species. In other words, vertebrates (including humans) share neural mechanisms capable of

processing an *interspecific* range of communicatively significant acoustic signals. These mechanisms are at levels higher than the purely auditory, but lower than the species-specific-vocal (e.g. the "phonetic" level in humans). The term "bio-communication" (Scanlan, 1988) is used below in referring to such levels of analysis and to the acoustic cues which receive special attention there. The involvement of "bio-communication" mechanisms in the perception of certain speech sounds could explain similar patterns of categorisation by both human and non-human listeners. The arguments against such categorisation occurring at a more peripheral "auditory" level are detailed below.

This "neuroethological" approach to speech perception (Suga, 1988) has the potential to reveal some aspects of the phylogeny of speech. For example, within the framework of a divergent evolutionary model, the data presented here could indicate a common antecedent for the budgerigar form (FM pattern of contact calls) and the human form (FM pattern of formant transitions) of a particular "bio-communication cue". Focusing on the present study of human/budgerigar vocal interaction, a shared level of communication-sound processing would explain not only the budgerigar's ability to substitute components of budgerigar warble into speech imitation sequences (and components of speech imitation into warble sequences), but also the human listener's ability to interpret these performances as "speech".

Formant transitions

A major problem for speech researchers is the apparently invariant perception of phonemes represented by highly variable acoustic patterns. A classic case of such acoustic variability is that of stop consonants in consonant-vowel (CV) syllables. Perceptual experiments such as those by Liberman *et al.* (1954) and Liberman (1970) showed that formant transitions - particularly F2 transitions - could convey sufficient information to distinguish place of production (for example, to distinguish a bilabial stop like /b/ from an alveolar stop like /d/ in the contrasting pair /ba/- /da/). In two-formant syntheses of pairs like /di/- /du/, however, in which the same consonant is followed by different vowels, the F2 transitions cueing the identical-sounding /d/ segments differ greatly between the two syllables, their contours being determined by the F2 frequencies of the following vowels (Liberman *et al.*, 1967). Is there, then, an invariant property of the signal corresponding to the invariant perception of /d/?

The traditional approach to this problem in relation to stop-consonant place of production (e.g. by Blumstein and Stevens, 1979) has been to focus - with inconclusive results - on spectral features,

which are presumed to engage purely auditory mechanisms of perception. The discovery that non-human subjects (Japanese quail, *Coturnix coturnix* - Kluender *et al.*, 1987; rhesus monkeys, *Macaca mulatta* - Morse and Snowden, 1975; other macaques, *Macaca fasciata* and *M. nemistrina* - Kuhl and Padden, 1983; chinchillas, *Chinchilla laniger* - Miller and Kuhl, 1976) could also discriminate among stop-consonant stimuli according to place-of-production categories reinforced the view that such discrimination relied on purely auditory processes. However, continuing research (e.g. by Tomiak *et al.*, 1987; Kewley-Port *et al.*, 1988) has indicated that, at least in humans, there is no "special" processing of speech (such as the imposition of perceptual categories) at auditory levels. Indeed, there is strong neurophysiological evidence that, at these levels, processing of speech and non-speech sounds is identical. Sharma *et al.* (1993) recorded an event-related potential which is sensitive to fine acoustic differences while subjects listened to stimuli comprising a /da/-/ga/ continuum. They found that the response was the same for stimulus pairs within and between categories, indicating that there is no categorical effect at auditory levels. The experiments of Kluender and Diehl (1987) and Kluender *et al.* (1987), which could identify no invariant acoustic correlates of the speech categories perceived by Japanese quail, support the view that in some non-human species, too, processing of such categories does not occur at purely auditory levels.

This, then, is the situation: there is a large body of experimental evidence which indicates that some communicatively significant components of speech are processed similarly in humans and some non-humans. Also, there is a range of evidence which refutes the view that such processing occurs at purely "auditory" levels. The conclusion from these findings is that this processing must occur at more central levels - levels which afford some "special" treatment to communication sounds. These levels must be intermediate between "auditory" and, e.g., (in humans) "phonetic" or (in birds) "song-specific" levels, because they are capable of processing *interspecific* communication sounds. This is possible because some communicatively significant acoustic cues are common to the vocalizations of a variety of vertebrates. These acoustic cues, which allow components of one species' communication sounds to be processed as "communicatively significant" by an individual of another species, can be isolated by the study of phenomena such as avian "speech". The "bio-communication cue" examined in this paper is a particular pattern of frequency modulation which is a communicatively essential component of both the /i/ vowel in human speech and the budgerigar contact call. A budgerigar's processing of this cue at the "bio-communication" level allows it to identify the /i/

sound with the species-specific call in communicative behaviour with a human companion.

At the same time as the speech scientists were investigating the putative "auditory discontinuities" of speech perception by perceptual experiments with animals, comparative neurologists were beginning to develop models of speech perception based on findings relating to central perceptual mechanisms in non-human species. A concept basic to these models is that of the "neural map". One such neuroethological model has been constructed - significantly for the present argument - by analogy with an avian perceptual mechanism. Sussman (1989) has proposed an analogy between the categorical perception of speech sounds by humans and sound localization in the barn owl (*Tyto alba*). The essence of his argument is that, by the co-activation of an *array* of neurons, individual speech sounds can be located within a multi-dimensional neural map of speech-sound categories in much the same way as perceived sounds can be located within the barn owl's neural map of external space (Knudsen and Konishi, 1978).

This model of speech perception is in line with the hypotheses of Suga (1988), who discovered arrays of neurons in the auditory cortex of the moustached bat (*Pteronotus parnellii*) which responded to combinations of biologically significant parameters in the bat's echolocation vocalisations (Suga *et al.*, 1978). Suga hypothesised that speech perception could be based on a spatio-temporal pattern of neural activity which, by such "neural mapping" of communicatively significant acoustic signals, operates in a fashion analogous to the perception of echolocation calls by bats. He (Suga, 1988) endorsed a neuroethological view of acoustic communication in which the uniqueness of a species' system for the perception of biologically significant signals is, nevertheless, based on the specialization of shared mechanisms. He pointed out that many bio-communication sound systems, including human speech, are composed of three types of information-bearing elements: constant frequency (CF), noise burst (NB) and frequency-modulated (FM) components. For example, the consonant-vowel syllables of English consist of a plosive burst (NB), formant transitions (FM) and vowel formants (CF). The CF and FM components of these sounds have a similar acoustic structure to the sonar signals of moustached bats, and could therefore be processed by analogous mechanisms.

Suga (1988) also points out that the classical methods of auditory physiology, in which neural responses to pure tones and clicks are elicited, has contributed little to our understanding of central auditory mechanisms. He advocates a neuroethological approach - using biologically significant sounds - for the study of the central auditory

system. In the spirit of this plea, Cynx *et al.* (1990) related CF and FM cues in the harmonic spectra of zebra finch song syllables to the formant structure of human speech, and suggested that this acoustic correspondence might be related to central rather than peripheral auditory mechanisms.

Thus the human-like results of speech-perception tests with non-human animals could result from the higher-order processing of these sounds in auditory centres designed for the processing of species-specific signals similar to speech in their information-bearing (or "bio-communication") parameters. The demonstrated capacity of a budgerigar to substitute communicatively significant elements of speech for acoustically similar elements of species-specific song in its vocal repertoire indicates the possibility of such common auditory mechanisms for the processing of communication sounds. (In the case of the budgerigar, however, even the highest-level centres have been able to adapt, as a result of vocal learning, to process speech as if it were budgerigar sounds. See Margoliash, 1983, for evidence that single units in songbird HVC - the "higher vocal centre" of the telencephalon - respond to specific song syllables which the bird has learnt as part of its repertoire even when, as a result of contrived learning conditions, those syllables are untypical of its natural song.)

The hypothesis presented here is that there is a level of analysis which handles bio-communication sounds in an integrative, categorical fashion - extracting information from parameters which vertebrate communication sounds have in common before the sounds proceed to the highest, species-specific levels of analysis. In species which learn their vocalizations, like some birds, these highest levels, too, can be modified by learning experience to process alien sounds as if they were species-specific. This is possible, however, only because of the lower-level function of interspecific bio-communication cues.

The voicing distinction

The most intensively-studied example of "special" processing in speech perception - by both human and non-human subjects - is the categorical discrimination of voiced and voiceless initial stop consonants in CV syllables. A synthetic continuum of sounds between English /ba/ and /pa/, for example, is perceived by English speakers as consisting of a group of virtually indistinguishable /ba/s and a group of virtually indistinguishable /pa/s, with a marked contrast between the two groups. Stimuli adjacent to each other in the continuum, but which fall on opposite sides of the perceptual boundary, are clearly distinguishable. The physical variables in this case are connected with a

contrast in the onset of laryngeal vibration, which occurs near the beginning of the sound in /ba/ and after a delay of more than 20 msec in /pa/. (See Liberman, 1977, for a discussion and review.)

The discovery of this phenomenon was initially regarded as evidence of speech-specific mechanisms in human auditory perception, and was even embraced by proponents of the "motor theory" of speech perception (Liberman *et al.*, 1967; Mattingly *et al.*, 1971; Liberman and Mattingly, 1985; Mattingly and Liberman, 1988), which seeks to link the perception of speech sounds with knowledge of the articulatory gestures involved in their production. Experimental evidence that prelingual infants imposed the same perceptual categories on the stimuli (reviewed by Kuhl, 1987, 1988, 1989) countered the arguments of the motor theorists, while studies with infants exposed only to languages which do not employ the voiced/voiceless contrast provided evidence for an innate, universal sensitivity to this distinction (Lasky *et al.*, 1975; Streeter, 1976; Eilers *et al.*, 1979).

Comparable results from several species of nonhuman vertebrate (rhesus monkeys - Waters and Wilson, 1976; Japanese macaques, *Macaca fuscata* - Kuhl and Padden, 1982; chinchillas - Kuhl, 1976, 1979, 1981, Kuhl and Miller, 1975a, 1975b, 1978; budgerigars - Dooling *et al.*, 1987, 1989, 1995, Dooling and Brown, 1990) have indicated that the phenomenon is not even *homo*-specific. When both identification and discrimination of the stimuli have been tested, the animal results have dovetailed in the fashion considered necessary and sufficient evidence for the categorical perception of speech (Studdert-Kennedy *et al.*, 1970) - the peak in the discrimination function corresponding with the discontinuity in the labelling function (Kuhl, 1981; Kuhl and Padden, 1983). (These results are reviewed, and their implications discussed, by Miller, 1977; Kuhl, 1979, 1986a, 1987, 1988, 1989; Snowdon, 1979, 1990; Moody *et al.*, 1990.)

Finally, correspondences between VOT as *produced* by speech-imitating birds and by their human trainers have contributed to speculation about common underlying perceptual mechanisms (Scanlan, 1988; Patterson and Pepperberg, 1998).

The difference in timing between the onset of laryngeal vibration and the plosive noise burst in syllable-initial prestressed stop consonants is known as "voice onset time" or VOT (Lisker and Abramson, 1964). On spectrograms of English stop consonants the beginning of laryngeal vibration is most clearly reflected in the onset of first-formant (F1) excitation, as there is little pre-voicing aspiration noise at first-formant frequencies. A voiced/voiceless continuum can, therefore, be synthesised simply by "cutting back" the first formant as the stimuli move from voiced to voiceless (Liberman *et al.*, 1958). The

stimuli in all the animal experiments have been of the "F1 cutback" variety - in which, as in speech itself, the onset frequency of F1 is a spectral correlate of the temporal cue. (Soli, 1983, has argued that this spectral feature is critical for human subjects. See Rosen and Howell, 1987, for a review of the debate about spectral and temporal cues for VOT.) Thus these experiments, while demonstrating categorical perception of voiced/voiceless consonant continua in non-human vertebrates, do not isolate timing differences as the sole criteria for the distinction.

Sinex *et al.* (1991) emphasised the importance of spectral cues in the categorical response of auditory-nerve fibres to an "F1 cutback" /da-/ta/ continuum which they recorded in chinchillas. An analogous peripheral response to the same stimuli in humans has been suggested by the recording of cortical auditory evoked potentials (Sharma and Dorman, 1999). The integration of cues resulting from auditory sensitivities at the periphery could occur at the hypothesised "bio-communication" level of processing.

The variable, inverse relationship between spectral and temporal cues has become known as "trading relations" (e.g. in Best *et al.*, 1981; Repp, 1982; Sinnott and Brown, 1997). Best *et al.* (1981) interpreted this "perceptual equivalence" of cues from different acoustic dimensions as indicating that these acoustic cues are processed phonetically, and found that such processing did not occur when listeners perceived the acoustic variations as nonspeech contrasts. They went on to argue that this "equivalence" of the acoustic cues at the phonetic level indicates that, at that level, the common articulatory origin of the two cues is taken account of. This view (in accord with that of Repp, 1982) falls within the ambit of the "motor theory" of speech perception: see, e.g., Liberman and Mattingly (1985). Unfortunately for the motor theory, however, it has been shown that Japanese quail have a human-like compensatory response to covariations in F1 onset frequency and F1 cutback duration in the perception of CV syllables (Kluender, 1991; Kluender and Lotto, 1994). Similarly, Sinnott and Brown (1997) have found comparable trading relations between spectral and temporal cues in the perception of /ra-/la/ continua by Japanese macaques.

Recently, Lotto *et al.* (1997) have tackled the problem by hypothesizing that, as uniform physical laws operate on all the vocal mechanisms in the animal kingdom, individuals are specially sensitive to the manifestation of certain physical constraints on vocalization - even in the sounds of an alien species. (They were discussing their finding that in Japanese quail the perceptual boundary within a /da-/ga/ continuum changes, in response to changes in a preceding syllable, in

the same way as it does for human subjects. In humans, this effect is known as "perceptual compensation for coarticulation".) The approach of Lotto *et al.* is, in effect, an attempt to accommodate the animal results within a kind of species-general motor theory. Considering the fundamental differences between the mechanisms of vocalization in birds and humans, however, it is not possible to invoke even the most generalised motor theory in explaining inter-specific neural patterns for the perception of human and avian vocalizations. In this case, at least, an emphasis on auditory rather than motor factors in explaining the phenomena seems inevitable. The adult-like perceptual performance of prelingual infants (e.g. Kuhl, 1989) is strong evidence that here, too, auditory factors must be predominant.

An attempt could be made to incorporate arguments such as those of Lotto *et al.* into a "direct realist" theory of speech perception, which argues that perception of all sounds - speech included - can be considered as *direct experience* of the sound source rather than (as in the motor theory) a *cognitive reconstruction* of the sound source (Fowler, 1980, 1986, 1990, 1992). The attempt would probably founder, however, in the conundrum of "direct" perceptual experience of a songbird's syringeal mechanism.

Alternatively to the motor theory or direct realist interpretations, and more in accord with the body of evidence adduced in this paper, trading relations (and perceptual compensation for coarticulation) could be seen as reflecting the complex activity of a multi-dimensional "neural map" of communicatively significant acoustic cues similar to that hypothesised by Suga (1988) and discussed above. In this case, processing at intermediate "bio-acoustic" levels could be similar in humans and animals, and explain the human-like categorical response of animals to some speech-sound stimuli.

Vowels

Vowel sounds have traditionally been regarded as discriminable on the basis of static spectral features (Peterson and Barney, 1952; see Rosen and Fourcin, 1986, for a review and critique of this position, and Miller, 1989, for its elaboration into an "auditory-perceptual theory" of the vowel). A long-established principle of acoustic phonetics is that the *relationships* among formant frequencies are of prime significance in vowel discrimination (Potter and Steinberg, 1950). Scheich *et al.* (1977) remarked on the significance of "formant" structure (relative position of spectral envelope peaks) in vertebrate vocalizations generally, and, in a later paper (Scheich, Bonke and Langner, 1979), focused on the formant structure of human vowels and the ability of

individuals of other species (chinchillas - Burdick and Miller, 1975; dogs - Baru, 1975; cats - Dewson, 1964; monkeys - Dewson *et al.*, 1969) to discriminate among them. Such discrimination had been shown to be based, as in human vowel perception, on formant-frequency relationships (Baru, 1975; Burdick and Miller, 1975). This has been corroborated by more recent work with baboons, *Papio anubis* (Hienz and Brady, 1988) and macaques and vervet monkeys, *Cercopithecus aethiops* (Sinnott, 1989). On the other hand, the work of Kuhl (1991) has suggested that, for human listeners but not for rhesus monkeys, there may be within-category distinctions relating to "prototypical" vowel sounds. Recordings of event-related potentials reflect the multi-faceted nature of human speech perception (Aaltonen *et al.*, 1987; Naatanen *et al.*, 1997), as incorporated in recent attempts at "connectionist" (or neural network) modelling of such perception (reviewed in Protopapas, 1999).

Scheich and his colleagues recorded neuronal responses to both natural and synthetic vowel sounds in tonotopically organised layers of telencephalic Field L of speech-trained Indian hill mynahs. They reported (Langner *et al.*, 1979) that some units responded selectively to only one or two vowels, while many units could distinguish between two vowels which shared a common formant frequency. This approach revealed a variety of excitatory-inhibitory interaction patterns in the selective responses of individual neurons to two-formant stimuli. When plotted in relation to F1 and F2, these neuronal responses (Langner *et al.*, *ibid.*) corresponded with discrimination patterns derived from human psychophysical responses to the same vowels (Hose *et al.*, 1983). This indicates a similar neural perception mechanism for these human sounds in both man and mynah (Hose *et al.*, *ibid.*). The hypothesis of Langner *et al.* (1981) that this vowel-specific response in the birds' forebrains was because of their speech-learning experience, while in line with the argument of this paper, remains to be tested. Meanwhile, my own analyses of speech-imitation sounds by several species of "talking" birds (Scanlan, 1988), and analyses by Patterson and Pepperberg (1994) of the "speech" of an African grey parrot (*Psittacus erithacus*), indicate that formant frequency relationships are distinguishing features of vowel imitations *produced* by birds, and that therefore they are *perceived* as such.

The ascending perceptual pathway in the Guinea fowl (*Numida meleagris*) involves auditory midbrain nuclei whose neurons are responsive to complex acoustic cues used in species-specific communication sounds but are unable to discriminate among such sounds (Scheich *et al.*, 1977). The Guinea fowl's telencephalic auditory nucleus (Field L), on the other hand, contains units which can

discriminate among call types (Bonke *et al.*, 1979; Scheich, Langner and Bonke, 1979). These findings suggest a hierarchical pattern of auditory perception in which "bio-communication cues" are identified before the complete communicative analysis of the signal. (Significantly, the Guinea fowl vocalization which was the subject of these studies, the "iambus call", has an acoustic structure similar to that of human vowels - Scheich, Langner and Bonke, *ibid.*) Field L of the Indian hill mynah is similar in structure and function to that of the Guinea fowl (Langner *et al.*, 1981), which suggests that there could be a corresponding identification of "bio-communication cues", such as the presence of formant-like peaks in the spectrum, at midbrain levels in the mynah before the complete analysis of, e.g., vowel sounds in the forebrain. That the response of non-human animals to vowel formant patterns is not the result of simply acoustic neural processing is suggested by the finding that in some birds (Hienz *et al.*, 1981) and monkeys (Hienz and Brady, 1988; Sinnott and Kreiter, 1991) acuity of vowel discrimination is far greater than that expected on the basis of pure-tone discrimination ability.

The patterns of neuronal response to species-specific calls in Guinea fowl, and human vowels in Indian hill mynahs, correspond to those (discussed above) which Knudsen and Konishi (1978) found in sound-localizing barn owls, as well as those which Suga discovered in echolocating bats (Suga *et al.*, 1978) and those which he (Suga, 1988) hypothesised as being involved in human speech perception. The results of psychophysical tests of human vowel perception by Hose *et al.* (1983) support Suga's hypothesis.

Scheich *et al.* (1983) considered the presence of such neural auditory response patterns in a diversity of vertebrates, in which "each individual call will lead to a distinct spatial pattern of excitation of small ensembles of neurons", as being evidence of their phylogenetic stability. These homologous auditory mechanisms could have resulted in the evolution of a variety of species relying on similar acoustic cues in vocal communication (Scheich, 1985). Reciprocally, the communicative effectiveness of these acoustic cues, and therefore their phylogenetic conservation, could explain the remarkable stability of the auditory system throughout vertebrate evolution (Scheich *et al.*, 1983).

GENERAL DISCUSSION

The evolution of speech

Assumptions about the evolution of speech underlie most

theorising on the basic mechanisms of speech perception. Advocates of "auditory sensitivities" (e.g. Kuhl, 1988) regard audition as primary, and the evolution of acoustic communication systems - including human speech - among the vertebrates as having been influenced by auditory factors which have been relatively stable, phylogenetically (Scheich *et al.*, 1983; Dooling *et al.*, 1995), and thus as having generally preceded and guided the evolution of vocal mechanisms. The "motor theory", on the other hand, with its emphasis on the primacy of production, regards the evolution of special auditory mechanisms for speech perception as having occurred subsequently to the evolution of the human vocal mechanism (Mattingly and Liberman, 1988), and the ontogeny of speech perception as being dependent on vocal experience (Liberman *et al.*, 1967).

Apart from the apparently insuperable problems for the motor theory posed by the animal and prelingual-infant experiments, the "auditory sensitivities" approach has the advantage of parsimony. Indeed, the idea that auditory systems involved in acoustic communication have evolved independently in various vertebrate classes and orders - and even genera and species (e.g. *Homo sapiens*) - is difficult to accommodate to any version of evolutionary theory.

The question then arises: do these "sensitivities" in humans relate to the general auditory system, or are they specially evolved for processing speech? Experiments with nonspeech sounds (e.g. those by Hirsh, 1959, Stevens and Klatt, 1974, Miller *et al.*, 1976, Pisoni, 1977, Divenyi and Sachs, 1978, and Jusczyk *et al.*, 1980, which all indicate a critical interval - analogous to VOT - in the perception of temporal order) have shown that categorical perception can apply to nonspeech stimuli. As Kuhl (1986b, 1987) has pointed out, however, these results could be interpreted in relation to the "tuning" of special speech-processing mechanisms - i.e., they may not be so narrowly tuned to speech as to exclude nonspeech sounds having the relevant features. Indeed Mattingly (1972), in comparing speech cues with sign stimuli such as the red belly of the male stickleback (see Tinbergen, 1951), emphasised the increased effectiveness of "supernormal" (i.e. artificially enhanced) cues in stimulating both speech-sound discrimination by humans and reaction to sign stimuli by animals.

Mattingly's insight, however, did not go beyond the level of comparing human speech cues with non-human acoustic signals such as avian alarm calls (which elicit stereotyped responses). The present paper argues, rather, that speech cues should be compared with features of avian vocalizations, such as certain frequency modulations in budgerigar warble song, which function contrastively within highly variable acoustic patterns to communicate specific information - such

as personal and group identity. (It is possible, nevertheless, that the communication cues of both human speech and budgerigar warble evolved from acoustic "sign stimuli" such as alarm calls.)

While animal speech-perception experiments demonstrate that mechanisms such as those underlying the perception of F2 transitions are not specific to humans, the research results presented in this paper indicate that, in budgerigars and humans at least, such shared mechanisms correspond to acoustic cues which have a shared *communicative* function. This conclusion is in line with those of Suga (1988), Cynx *et al.* (1990) and Dooling *et al.* (1995). The perspective advocated here is thus aligned to the "auditory sensitivities" view, with its Darwinian approach to the evolution of speech, but sees the phylogenetically stable element of the perceptual mechanism not as purely auditory, but as specially evolved to filter communicative components from incoming acoustic signals. The phylogenetic stability of this filter, and the conservation of acoustic "bio-communication cues" throughout phylogeny are, of course, complementary.

In focusing on their common, inherited features, this perspective adds new depth to a holistic view of vertebrate (including human) communication sounds.

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DECISION-MAKING AND TURN ALTERNATION IN PILL BUGS (*ARMADILLIDIUM VULGARE*)

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ABSTRACT: Twelve pill bugs (*Armadillidium vulgare*, Isopoda, Crustacean) were examined in 200 successive T-mazes. When obstacles are present, *A. vulgare* tend to move by means of turn alternation, which is generally considered an innate adaptive behavior. With a decrease in air moisture, the bugs have a tendency to increase their turn alternation rate. However, in such long successive T-mazes as in this study, continued turn alternation should actually accelerate the bugs' desiccation. This fact implies that turn alternation cannot always work adaptively. In this trade-off situation, while three individuals kept turn alternation at a high rate (1) and four at a low rate, (2), the other five spontaneously increased the rate of turn alternation and then decreased it (3). This instability of turn alternation in group (3) is interpreted as resulting not from stochastic factors but rather from the bugs' own decision-making, and seems to be an escape behavior used to get out of the experimental apparatus. In order to verify the decision-making hypothesis, all animals were subsequently tested in another successive T-maze apparatus, where the ends of the chosen alleys were shut, i.e., with 50 successive blind alleys. In this situation, while individuals of groups (1) and (2) continued to wander inside the apparatus, those of group (3) found a vertical rough wall, climbed it, and escaped from the apparatus in the middle of the experiment. Most of the unexercised individuals in the control experiment did not show climbing behavior.

Generally, a cornerstone of ethological theory is the understanding that behavior of animals comes in modal action patterns (MAP) (Barlow, 1977). MAP was introduced to soften the concept of fixed action patterns (FAP) (Thorpe, 1951) and is considered to explain the variability among individuals when performing a particular sequence of action patterns. It means that a MAP consists of a main adaptive stereotyped pattern resulting from a species-characteristic stable mechanism, and minor nonadaptive variant patterns resulting from individual-characteristic genetic variation. However, sometimes we encounter individuals for which the MAP cannot be identified, because

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the frequency of variant patterns is higher than or almost the same as that of the stereotyped pattern. For these individuals, we cannot discard the idea that such variant patterns may imply autonomous behavior resulting, not from innate genetic variation, but from decision-making. If so, in contrast to commonly accepted ideas, we can experimentally observe that such individuals spontaneously increase the variant patterns for adaptation. In this paper, by testing the movements of *A. vulgare*, the generation of variant patterns implying adaptability is demonstrated.

In an open field, *A. vulgare* move forward in a straight line (Iwata & Watanabe, 1957a). It is said that in natural settings, a linear path of movement is the most efficient adaptive strategy when the animal lacks precise information about environmental resources or hazards (Jander, 1975). When obstacles are encountered, a number of invertebrate species use turn alternation, i.e., a left turn followed by a right turn (or vice versa), to correct the deviations from linear movement (Hughes, 1989a). Such behavior has also been investigated in *A. vulgare* (Watanabe & Iwata, 1956; Iwata & Watanabe, 1957a, b; Kupferman, 1966).

It is suggested for terrestrial isopods that the mechanism underlying turn alternation is based mainly on proprioceptive information about the previous turn which arises in the process of turning from bilaterally asymmetrical leg movements (BALM) on the two sides of the body (Hughes, 1985, 1987, 1989b). The adaptive function of turn alternation has also been interpreted as an 'escaping' one ensuring efficient motion away from biologically unfavorable conditions, since it is intensified by desiccation or contact with a predator (Hughes, 1967; Carbines, *et al.*, 1992). Overall, when performing a sequence of action patterns, keeping turn alternations at a high rate constitutes an 'escape behavior' and can be considered as MAP. The stereotyped pattern in such a setup is each turn alternation, i.e., a pair of successive turns in opposite directions, based on a stable BALM mechanism. The variant patterns are those such as successive turns in the same direction, backtracking, and so on, based on individual genetic variation.

In extant studies, escape behavior was studied in only three or four successive T-mazes (e.g., Watanabe & Iwata, 1956; Hughes, 1967; Carbins *et al.*, 1992). In such short-path situations turn alternation may seem to work efficiently. In the present experiments, each individual experienced 100 successive T-mazes in each of two successive days (Experiment 1). In such long-path situations, continued turn alternation would result in water deficit in the body. Since, as described above, there is a tendency to increase turn alternation in response to desiccation, it can be seen that in this trade-off situation turn alternation

no longer works adaptively. This situation seems to present an unsolvable problem if one believes the MAP concept, i.e., that an intrinsic mechanism underlying turn alternation, BALM, is stable. But on the contrary, since the pill bugs are free from any observer's MAP concepts, it can be expected that they solve it by spontaneously discarding turn alternation, i.e., by increasing variant patterns after the spontaneous stabilization of turn alternation.

Recently, the generation of variant patterns has been observed as resulting in autonomous transformation of MAP in a trade-off situation, and was interpreted as 'behavioral plasticity' (Gunji, 1996; Migita & Gunji, 1996). In the experiment of rout-formation in pheromone-dependent ants, an excessive generation of pheromone-independent behavior triggered the transformation of the established route. Although such generation of variant patterns is usually considered as resulting from innate genetic variations, it was attributed to 'decision-making of the ant itself' (Kitabayashi & Gunji, 1997). Moreover, in a maze experiment, octopuses spontaneously increased variant patterns and used them for novel solutions in a maze with a trade-off condition (Moriyama & Gunji, 1997). If the increase of variant patterns of *A. vulgare* results not from innate genetic variations but rather from decision-making, which implies manifestation of their autonomous choice of action patterns, we should be able to observe the behavior's novelty and adaptability. In order to verify this hypothesis, a second experiment was performed (Experiment 2).

METHODS

Subjects

One hundred and fifty individuals of *A. vulgare* as a group were caught on a woodland path at the south foot of Mt. Rokko, Kobe, Japan (34°43' N, 135°14' E, 400 ft in altitude) in July for main stock and were kept in a plastic container (20 cm in diameter, with soil to a depth of 2 cm and an opaque thick paper lid) in the laboratory. They were fed with slices of carrot (Heeley, 1941). A moist atmosphere was maintained by wetting the soil every day. The lid was closed and illumination was off except for feeding and wetting (once in the morning). The temperature of the laboratory was kept at 23-25; the humidity was 30-40%.

In the experimental phase, some individuals, each of which was 8-9 mm in length and 4-5 mm in width, were selected from the main stock and placed one by one into petri dishes (8 cm in diameter, with a thin

layer of soil). Their ability to move actively on the horizontal floor and vertical wood wall (i.e., rough-surface wall) was also examined. Each individual was isolated and fed on a small piece of sliced carrot for 2 days prior to conducting the experiments. The condition of atmosphere and illumination were the same as in the main container.

General Procedure

On the third day, experiments were conducted. At first, each individual was placed into another petri dish without lid and soil and exposed to light for ten minutes. This sudden bright and dry condition provided the stimulus for motion. A 15-watt fluorescent light that had an intensity of 200 Lx at a distance of 100 cm from the floor of the dish was used as the light source. White paper pasted on the floor of the dishes removed the soil from their legs while they were moving around. Then each individual was placed into the experimental apparatus under the same brightness condition. Each experiment lasted for not more than 30 minutes ensuring no alternation in their behavior due to dehydration (Warburg, 1964). It was stopped when an individual stayed stationary for more than two minutes or escaped by getting over the wall of the apparatus. After each experiment, individuals were returned to their previous petri dishes with lid and soil. The behavior was recorded by CCD camera connected to a video recorder.

EXPERIMENT 1

Procedure

In order to construct long successive T-mazes, the apparatus shown in Fig.1 was devised. White paper was pasted on the runways to make the individuals move quickly (Hughes, 1992). Twenty individuals were selected and each one was safely lowered into the start alley of a T-maze. As soon as they passed the first T-junction, the corresponding turntable was rotated to lead them through the connection path to another T-maze. In this way, they were forced to continue moving from one junction to another. Locomotion from one junction to another was defined as one trial, and each individual was examined for 100 trials in the wooden wall maze (Fig.1) on the first day (Experiment 1A). In order to investigate that juxtaposition of rough and smooth walls does not cause climbing behavior on rough ones, the same individuals were also examined in the Teflon and partial wooden wall maze (Fig.2) for 100 trials on the next day (Experiment 1B).

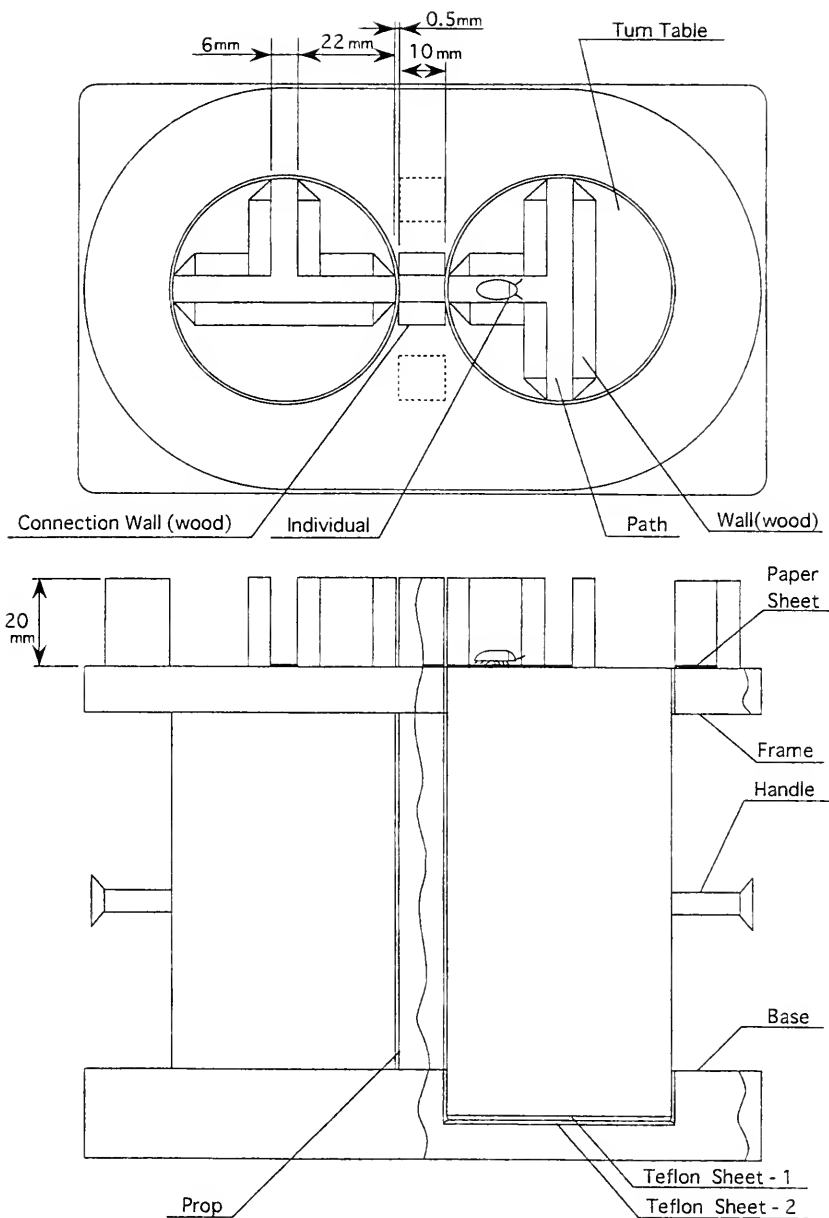


Figure 1. Apparatus implementing long successive T-maze with wooden walls. Each turntable mounts a T-maze, and has a handle to be turned manually. An observer can make each individual experience successive T-mazes by turning the turntables. As a result, each alley of the maze becomes 54 mm.

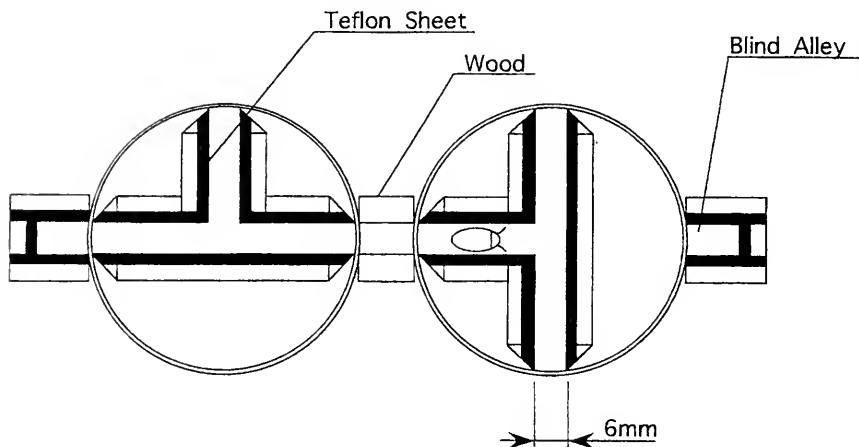


Figure 2. Apparatus implementing long successive T-maze with Teflon walls. All the walls except for the connection wall are covered with Teflon sheets. Notice that blind alleys with Teflon walls are used only for Experiment 2A and 2B, not for Experiment 1B. Other details are the same as in Fig. 1.

RESULTS - EXPERIMENT 1

A sequential action pattern of '2-3-4' in Fig.3 was defined as 'L-1', and '4-5-6' as 'R-1'. In this way, the second turn in an action pattern becomes the first turn of the next one. These turn alternations are the stereotyped patterns. The other patterns (6 patterns, R-2~R-4 and L-2~L-4), illustrated in Fig.4 were also observed. These constitute the variant patterns. The patterns R-3, R-4, L-3 and L-4, in which the individual begins to turn in one direction, and then reverses its choice and completes the turn in the opposite direction are distinguishable in this framework.

First, for the analysis of occurrence of L-1 and R-1, the total number of each pattern for each individual in each experiment was counted. Individual No.3 escaped after three trials in both Experiments 1A and 1B. Nos.8 and 10 stayed stationary for more than two minutes from the start in both experiments Nos. 9 and 15 started in motion, but in the middle of the trials (No.9, 10th trial in Experiment 1A, 23rd trial in 1B; No.15, 48th trial in 1A, 15th trial in 1B) stayed stationary for more than two minutes. As for Nos.6, 14 and 16, though they moved in all the 100 trials in Experiment 1B, they stayed put in the middle of

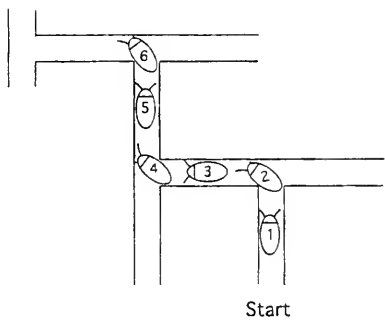


Figure 3. Illustration of turn alternation. The numbers indicate successive position as an individual moves. The individual is turning to alternating directions. ‘2→3→4’ is defined as ‘L-1’. ‘4→5→6,’ ‘R-1’.

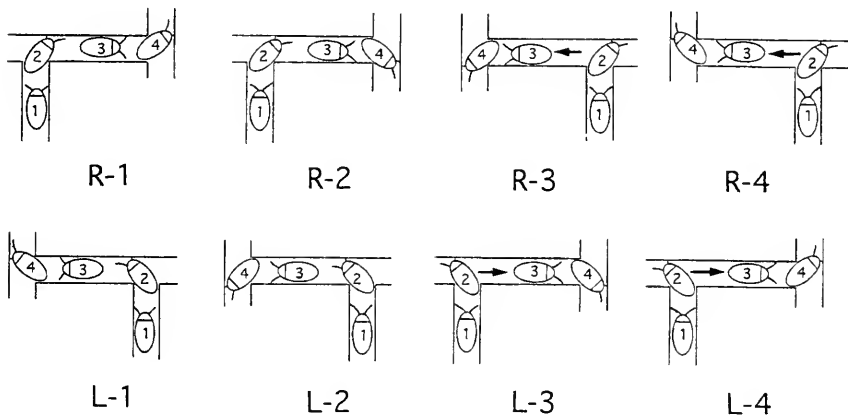


Figure 4. Variant patterns (L-2, 3, 4 and R-2, 3, 4), and stereotyped patterns (L-1 and R-1). The numbers show the time sequence for the locomotion of individuals. In L-3 (R-3) and L-4 (R-4), individuals begin turning to the left (right) at the choice point, but change direction before reaching the next turning point.

Experiment 1A (No.6, 35th trial; No.14, 21st trial; No.16, 8th trial). In order to perform a consistent analysis, the data corresponding to these eight individuals were discarded and the remaining twelve data were investigated (Tables 1 and 2). The juxtaposition of rough and smooth walls of the apparatus in Experiment 1B did not elicit climbing behavior. Since the total number of L-1 and R-1 in each experiment (the

Table 1. Number of Action Patterns in Experiment 1A. G-scores (resulting from log-likelihood ratio Goodness of Fit test) of 3.84 correspond to the threshold significance of P-value 0.05 (df = 1). Values in the tables larger than 3.84 mean that the number of L-1 or R-1 is significantly larger than 50% of the total number of 'left action patterns (L-1,2,3,4)' or 'right action patterns (R-1,2,3,4)'. ns, not significantly larger than 50%.

	No. 1	No. 2	No. 4	No. 5	No. 7	No. 11	No. 12	No. 13	No. 17	No. 18	No. 19	No. 20	Total
L-1	30	32	39	32	33	28	29	30	37	38	38	33	399
L-2	10	13	11	5	12	26	22	3	9	3	6	4	124
L-3	1	1	1	2	2	2	2	1	0	0	0	2	14
L-4	4	12	2	0	1	6	15	0	1	1	3	0	45
Total	45	58	53	39	48	62	68	34	47	42	47	39	582
G-score	5.1	ns	12.27	17.36	6.92	ns	ns	22.5	16.5	31.81	19.25	20.58	82.1
R-1	24	32	39	32	34	30	29	31	36	38	37	36	398
R-2	15	6	4	23	12	4	1	25	15	20	12	24	161
R-3	5	3	1	1	0	0	1	0	0	0	0	0	11
R-4	9	0	2	5	5	2	0	10	1	0	3	0	37
Total	53	41	46	61	51	36	31	66	52	58	52	60	607
G-score	ns	13.68	25.54	ns	5.78	17.47	28.14	ns	7.89	5.68	9.61	ns	59.8

Table 2. Number of Action Patterns in Experiment 1B. G-scores (resulting from log-likelihood ratio Goodness of Fit test) of 3.84 correspond to the threshold significance of P-value 0.05 (df = 1). Values in the tables larger than 3.84 mean that the number of L-1 or R-1 is significantly larger than 50% of the total number of 'left action patterns (L-1,2,3,4)' or 'right action patterns (R-1,2,3,4)'. ns, not significantly larger than 50%.

	No. 1	No. 2	No. 4	No. 5	No. 7	No. 11	No. 12	No. 13	No. 17	No. 18	No. 19	No. 20	Total
L-1	29	33	34	30	34	40	34	38	38	37	40	26	413
L-2	7	16	31	3	13	15	6	10	9	4	5	5	124
L-3	0	1	0	1	0	1	1	0	0	3	0	1	8
L-4	2	13	1	0	3	1	0	3	0	2	0	1	26
Total	38	63	66	34	50	57	41	51	47	46	45	33	571
G-score	11.08	ns	ns	22.5	6.63	9.55	19.36	12.8	19.25	18.29	30.99	34.03	118
R-1	28	32	33	31	32	40	35	39	38	39	40	26	413
R-2	31	6	1	30	15	4	21	9	15	14	15	36	197
R-3	0	0	1	0	1	1	0	0	1	0	1	0	5
R-4	5	0	0	5	3	0	4	1	0	1	0	6	25
Total	64	38	35	66	51	45	60	49	54	54	56	68	640
G-score	ns	19.53	33.19	ns	ns	30.99	ns	18.34	9.23	11.05	10.63	ns	54.8

right hand marginal column in each table) is statistically significant, MAP, i.e., escape behavior constituted by keeping turn alternations at high rate, can be observed. However, on an individual level, only three individuals (Nos.17, 18 and 19) maintained high frequency of stereotyped patterns in both experiments. This result indicates that turn alternation is not always stable over time.

Next, in order to analyze temporal stability of turn alternation, the frequency of occurrence of each stereotyped pattern for each individual was investigated. A set of ten successive action patterns was taken in time order and called a 'session.' The frequency of L-1 and R-1 in a session were calculated as:

$$\text{freq. of } L-1 = \frac{\text{Number of } L-1}{\text{Number } (L-1 + L-2 + L-3 + L-4)}$$

$$\text{freq. of } R-1 = \frac{\text{Number of } R-1}{\text{Number } (R-1 + R-2 + R-3 + R-4)}$$

For example, if an observed time series in a session is:

→(R-1)→(L-1)→(R-1)→(L-1)→(R-2)→(R-1)→(L-1)→(R-3)→(L-3)→(R-1)→
then, the frequency of L-1 = 0.75 and the frequency of R-1 = 0.67.

Frequency values were then plotted as shown in Figs.5, 6 and 7. Though the two experiments were conducted on different days, an interesting behavior appears in the plots of individuals No.1, 2, 5, 11 and 12 if we take the effect of their past experience into account and regard the two experiments as continuum (Fig.5). The time series of L-1 frequencies for Nos.2, 11, and 12, and those of R-1 for Nos.1 and 5 illustrate this behavior. In these plots, in spite of the very low initial values (under 0.5, except for No. 2 (0.6)), the frequencies reach even lower values (the first minimum values). After this, the frequencies gradually increase and reach the first value of '1' (the first maximum value). In this time interval, i.e., from the initial value to the first maximum value, each of these individuals' frequencies significantly increases (See the results of Spearman's rank correlation test for each graph in the caption of Fig.5).

This kind of spontaneous increase of turn alternation, which is characterized by the overall increase in frequency of stereotyped patterns with a local minimum (first minimum value), was found only for these five individuals. Especially for Nos.1, 11 and 12, one can see

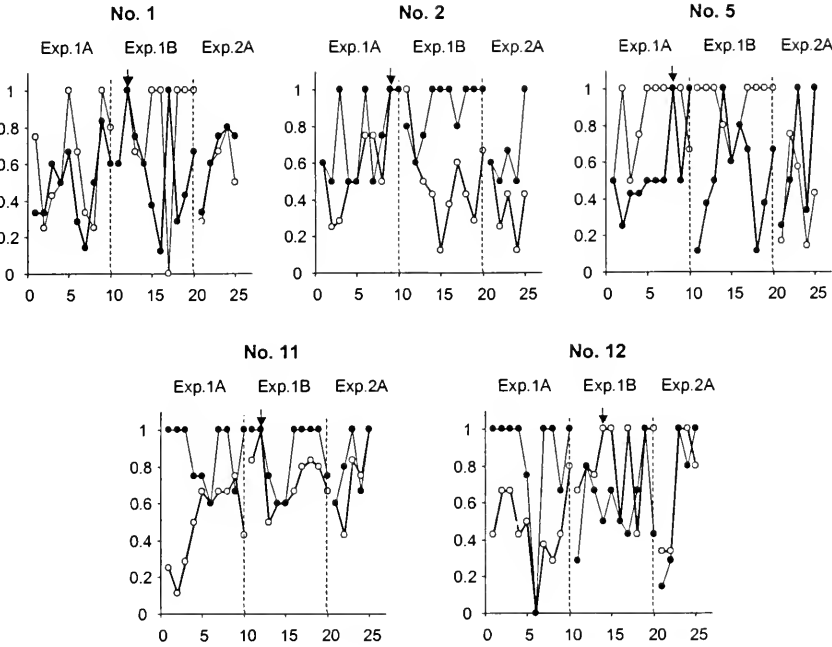


Figure 5. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the generative variation group (Nos.1, 2, 5, 11 and 12). Vertical axis represents ‘frequency’. Horizontal axis represents ‘session’. Individual subject number is shown at the top of each graph. The first maximum value (the first value of ‘1’) is indicated by the arrow. The behaviors of action patterns which show the tendency of spontaneous increase are emphasized by bold lines. The values of Spearman rank correlation coefficient (r_s), sample size (n) and significance level (p) are (individual subject number (r_s , n , p)); No.1 (0.5244, 12, <0.05), No.2 (0.6125, 9, <0.05), No.5 (0.6845, 8, <0.05), No.11 (0.8252, 12, <0.01), No.12 (0.5308, 14, <0.05).

that the values continue increasing from Experiment 1A to 1B despite different days, and reach ‘1’ in Experiment 1B. Importantly, just after this process, the frequency of each stereotyped pattern abruptly decreases again, i.e., the frequency of variant patterns increases, and reaches a value below 0.5. In this paper, these five individuals are called ‘generative variation group.’ Nos.17, 18 and 19, which maintained a high frequency of stereotyped patterns in both experiments, are called the ‘stereotype group, (Fig.6)’ and the other four individuals, the ‘error group (Fig.7).’

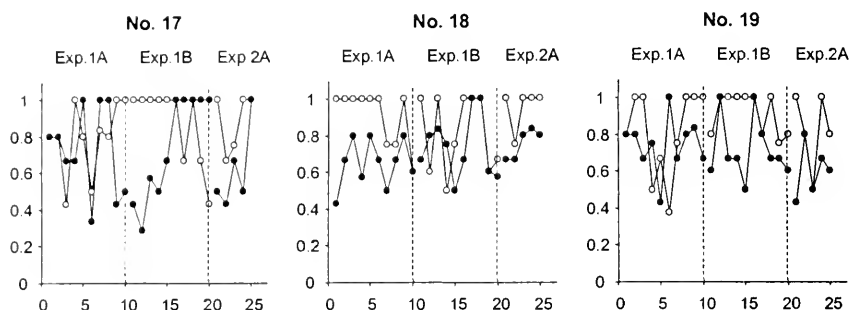


Figure 6. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the stereotype group (Nos. 17, 18 and 19). Vertical axis represents 'frequency'. Horizontal axis represents 'session'. Individual subject number is shown at the top of each graph.

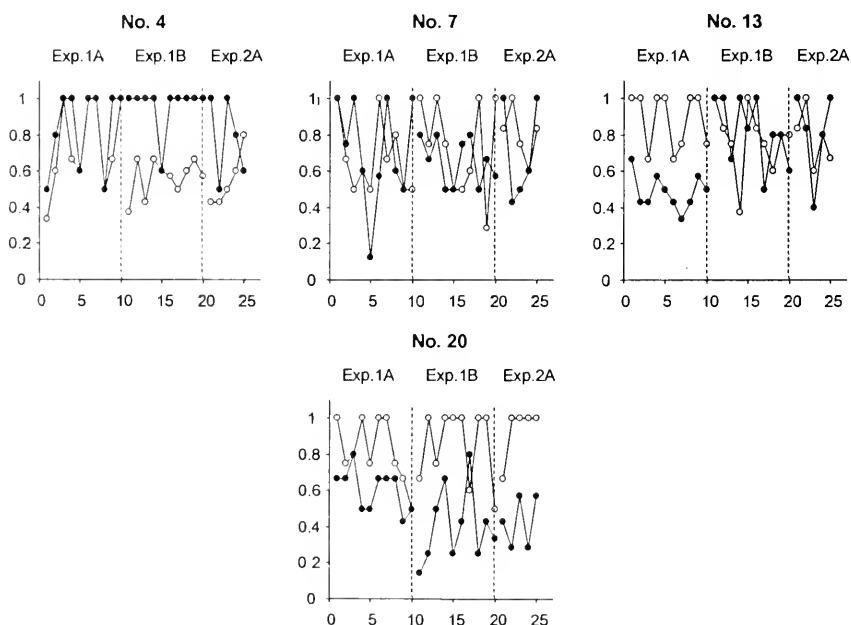


Figure 7. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the error group (Nos. 4, 7, 13 and 20). Vertical axis represents 'frequency'. Horizontal axis represents 'session'. Individual subject number is shown at the top of each graph.

In order to verify whether such an increase of variant patterns in the generative variation group results not from innate genetic variations but rather from decision-making, i.e., to verify the novelty and adaptability of the increase of variant patterns, a second experiment was performed.

EXPERIMENT 2

Procedure

The day after Experiment 1B, the same twelve individuals were examined in the same maze again. In this case, after passing the fifty-first T-junction, they were led to the blind alley situated at the end of the selected arm (Fig.2). Teflon sheets were also pasted on the walls of the blind alleys, because pill bugs climb walls at corners as a result of excess movement of forward-going-tendency, as do centipedes (Shafer, 1976). Then they were expected to backtrack and move to the next T-maze on the other turntable. After turning at the next junction, they were led to the opposite blind alley. In this manner, they were led into blind alleys successively for fifty trials (Experiment 2A). Moving around in this apparatus would only result in water deficit in their body. In this experiment, since two successive turns were precluded by the blind alley, individuals could not constitute escape behavior based on turn alternation or on variant patterns shown by the generative variation group in Experiment 1. In this situation, another novel escape pattern was required for survival.

Another twenty unexercised individuals were selected from the main stock and examined in a control experiment with the same apparatus under the same conditions. This experiment was implemented to investigate that the Experiment 1 with trade-off situation essentially effects on the generation of the novel behavior. These individuals were led to the blind alley from the first trial and ran into the blind alleys for fifty trials (Experiment 2B).

RESULTS - EXPERIMENT 2

As shown in Table 3, in Experiment 2A all individuals from the generative variation group noticed the wood wall in the connection section and climbed it in the middle of the trials (No.1, at 5th trial; No.2, 14th; No.5, 11th, No.11, 13th; No.12, 6th). The other individuals, except for No.7, did not climb the wall and continued moving around

the apparatus. No.7 escaped at the 7th trial. Generally, woodlice climb vertical walls for transpiration only in the case of saturated air conditions, as the higher location has lower humidity (Den Boer, 1961). In experiment 2B, sixteen of eighteen unexercised individuals continued moving around. The remaining two climbed the connection wall (also Table 3).

Table 3. *P* values (a.- c.) from Fisher's exact probability test.

	Climbing	Wandering	<i>P</i> value
Generative variation group	5	0	a. $p = 0.0006$
Stereotype & Error group	1	6	b. $p = 0.4657$
Total	6	6	c. $p = 0.0242$
Unexercised individuals	2	16	

The number of climbing individuals in Experiment 2B is significantly smaller than that of wandering ones (bottom row of Table 3; Binomial test: $p=0.0105<0.05$). This result reflects well the fact that individuals in this experiment are not climbing the wall for transpiration. However, despite this inhibitory condition for climbing, the portion of climbing individuals was significantly larger for those which experienced Experiment 1 than for the unexercised group (statistical test (c) in Table 3). This result shows that experiencing the trade-off situation (long successive T-mazes) caused some individuals to spontaneously climb a wall. Moreover, this behavior was by individuals in the generative variation group, not by those in the stereotype and error group (statistical tests (a) and (b) in Table 3). From these results, the climbing pattern in the generative variation group can be regarded as a novel one which does not result from innate factors, and also an adaptive one which provides a chance to seek moisture outside the closed apparatus. Thus emergence of the spontaneous increase of the variant patterns in Experiment 1 apparently functioned as novel and adaptive behavior.

DISCUSSION

In experiment 1, individuals were categorized into three groups: stereotype group, error group, and generative variation group. The behavior of both the stereotype group (Fig.6) and error group (Fig.7) are predictable from the MAP concept based upon BALM and innate genetic variation among individuals. Stable BALM with minor genetic variation can be inferred from the high rate of turn alternation in the stereotype group. Excess genetic variation in BALM can be inferred from the low rate of turn alternation in the error group. In the generative variation group, a spontaneous increase and subsequent decrease of turn alternation (i.e., a subsequent increase of variant patterns) were observed (Fig.5). This behavior is unpredictable from the MAP concept. In the MAP concept, a hidden innate 'BALM-correcting mechanism' is used to explain the observed increase in the turn alternation rate. But existence of this mechanism would cause the generative variation group to maintain the high turn alternation rate, when in fact variant patterns subsequently increased – a behavior regarded here as 'spontaneous.' Experiment 1 was constituted as problematic situation which cannot be solved by turn alternation; the solution requires that the individuals spontaneously discard this pattern of turning.

As there later appears to be a 'novel escape pattern' used to get out of the experimental apparatus, the increase of variant patterns in Experiment 1 can be considered the manifestation of decision-making. This is in contrast to the view where such variant behavior is considered as resulting from a hidden mechanism, or 'noise generator.' For example, in the theory of learning machines, the continuous process of learning (parallel here to increase of the turn alternation rate) altered by generation of noise (parallel to increasing of variant patterns) is a typical way of learning for a Boltzmann Machine (Ackley, *et al.*, 1985). In these machines, the objective of learning is to decrease the energy of the system. A noise generator stochastically provides heat as a noise source for increasing the energy, while the machine searches for lower energy states. In such a stance of general computational learning theory, noise never becomes an adaptive behavior.

However, in Experiment 2A, the climbing pattern, which is considered a variant pattern in regular conditions, spontaneously appeared and became an adaptive one in the generative variation group. The fact that the appearance of this pattern correlated well with that of the increase of variant patterns in Experiment 1 strongly indicates that such variant patterns in Experiment 1 did not result stochastically from an innate 'learning-machine' mechanism, but rather were generated as novel escape patterns. Decision-making in *A. vulgare* was thus

manifested as the spontaneous increase of variant patterns in the trade-off situation. This aspect of behavior has also been observed in maze learning by octopuses, and was called 'autonomous learning' (Moriyama & Gunji, 1997). In that experiment, a novel maze solution which could not result from 'machine learning' appeared in correlation to an increase in variant patterns. While such clear adaptability was not observed in the stereotype and error groups, the difference may result from the extent of their capacity to destabilize MAP.

Other explanation could be considered for the emergence of the variant patterns in Experiment 1 and the climbing pattern in Experiment 2. For example, one could infer that, if individuals of the generative variation group have an innately higher capacity to be well hydrated, they might have been saturated while being prepared in the petri dishes. Since this would be essentially the same condition as saturated air, they would not need to perform turn alternations in Experiment 1, and so tried to climb the wall for aspiration in Experiment 2A. If such individuals existed, the same ratio of climbing individuals should appear in the control in Experiment 2B. However, as shown in Table 3, only two of eighteen unexercised individuals demonstrated climbing behavior, while six of the twelve that had experienced long successive T-mazes did so.

In this paper, decision-making in such simple animals as pill bugs has been suggested. The evidence of their decision-making can be found in their autonomous destabilization of MAP. At first glance, the idea of decision-making seems to contradict the concept of MAP itself. But the relationship between MAP and variant behavior is like the head and tail of one coin; we have individuals of the stereotype group, and, at the same time, we can verify the adaptability of variant behavior. What this paper calls into question is the assumption that there is an innate stable mechanism underlying MAP – a belief whereby a new innate stochastic genetic variation is necessarily inferred to explain any variant behavior. Once such a concept of 'stable mechanism with stochastic variation' is adopted, variant behavior, which implies spontaneous transformation of MAP, has to be considered insignificant erroneous behavior.

Moreover, even when such cognitive behavior as learning is observed, it can be considered as resulting from an innate hidden higher mechanism, and so a concept like 'learning by instinct' appears (Gould & Marler, 1987). The machine learning theory tries to explain this by regarding animals as complex machines having several innate mechanisms; and only those with a brain or complex nervous system, producing different mechanism for various circumstances, are considered as performing flexibly and autonomously. This view implies that one can never discover novel behavior in animals. In this paper, the

potential instability of the MAP concept results from the experimental demonstration of an animals' decision-making behaviour.

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BOOK REVIEW

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Politics and People in Ethology: Personal Reflections on the Study of Animal Behavior, by Peter H. Klopfer, Lewisburg, PA: Bucknell University Press, 1999.

Peter Klopfer, self-defined ethologist and behavioral ecologist, provides us with a set of personal reminiscences spanning his long career in the study of animal behavior. Because of his belief that ethology "has been influenced as much...by the personalities and politics of its purveyors as by their data" (p. 11), he devotes much of the book to examining the personalities and/or politics of the teachers and researchers he has known. In so doing, he provides us with amusing anecdotes, historical accounts of various departments of psychology and fields of research, and his assessment of some controversial issues. A number of photographs enhance the text.

Because the book is, in many ways, an autobiography, we learn much about Klopfer's own personality and politics, as well. In the first chapter, "Personal Beginnings," he tells us how he came to adopt the Quaker faith, whose doctrines of pacifism and social activism are evident in the way in which he has lived his life. In the early 1950s, as a conscientious objector during the Korean War, he tore up his draft card. Fortunately, his a three-year prison sentence was reduced to probation, but he remained a convicted felon, which had implications later in his career. He was a student at UCLA at the time, and it was here that he met Martha Smith, who would later become his wife and partner, especially in his work with the social behavior of goats.

Klopfer devotes a chapter to the years he spent at Yale, where lasting friendships developed with G. Evelyn Hutchinson, who supervised his dissertation, and fellow graduate student Robert MacArthur. On receiving their doctorates both students took up post-

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docs in Britain, MacArthur at Oxford and Klopfer at Maddingley Field Station for Animal Behaviour at Cambridge. In the political climate of mid-1950s Britain, Klopfer soon was faced with the fact that the research of some scientists was "consciously driven by political ideologies" (p. 56). Was this the way to go? Klopfer decided that it was not, and took as his model Bill Thorpe, an eminent researcher and Director of the Field Station. Thorpe displayed "a politically neutral science complemented by a strong and faithful commitment to a particular social and political platform" (p. 56). Like Klopfer, Thorpe was a devote Quaker, and it was the values of this faith that both men exemplified. Indeed, over the years, the scientists with whom Klopfer developed the strongest rapport were usually Quakers.

With respect to the issue of the political use of one's research findings, Klopfer presents a very interesting examination of the controversy surrounding Konrad Lorenz's role in the Nazi policy of ethnic cleansing. He includes lengthy quotations from a 1940 paper by Lorenz that had not previously been published in English. Indeed, Klopfer suggests that Lorenz's hydraulic model of motivation, with its assumption that only a single, specific stimulus can release the motivated response, "may have been derived as much from this ideology as it was from his studies of animals" (p. 60). The link, of course, is the view that in order to maintain this species-specific behavior, hybridization should not occur. It was Lorenz's ebullient personality, Klopfer believes, that allowed colleagues to ignore his checkered past, as it seems Klopfer himself was willing to do.

In 1958, Klopfer accepted an appointment in the Department of Zoology at Duke University where he remains to this day. Like at least some other Duke faculty, he was attracted to the university by the sunny weather in North Carolina. The chapter on Duke describes his social activism, including his role in sit-ins and other activities of the anti-segregation movement, and in establishing the Carolina Friends School. At Duke, Klopfer soon developed ties with colleagues in the Psychology Department who were also studying animal behavior. Of interest to all primatologists is the account of the origins and early years of the Duke Primate Center. Associated with this is the sad story of the Center's co-founder, anthropologist John Buettner-Janusch, whose life ended in tragedy and despair.

A chapter is devoted to the research carried out, and the colleagues he worked with, on numerous field trips that took him from the Caribbean and Central America to Aldabra, an isolated atoll in the Indian Ocean. From the time he was at Yale, Klopfer and his wife raised goats, and studied their behavior. The Aldabra research involved the study of goats indigenous to the island. Included as an Appendix is

a Journal that he and Martha kept during their six-week field trip. A trip to Madagascar was made to confirm, in the field, results on maternal behavior obtained from captive lemurs at the Primate Station. This confirmation of findings with free-ranging animals has been a consistent theme of Klopfer's research.

In the chapter entitled "Later Years," Klopfer returns to the issue of science and values, as he presents his perspective on the stormy political debates that arose in response to the publication of E. O. Wilson's *Sociobiology*. He also deals with the history of the field of behavioral ecology with which he feels closely allied. And he looks back, longingly it seems to me, to the early days of ethology, when international meetings of the Ethological Conference were small, and young scientists were able to interact on a personal level with the luminaries of the discipline. The book concludes with Klopfer's reflections on his teaching, the social construction of ethology and the future of the field.

My only concern stems from the nature of the book: a set of reminiscences. As Klopfer himself points out, memory, one's own or that of one's colleagues, can be fallible. The book is filled with historical information, but it may be of little use to historians of science. I'm basing this conclusion on one example about which I have some knowledge of the history. This is the discussion of the relationship of Klopfer's friend, Donald Adams, with parapsychologist J. B. Rhine, both at one time member of the Duke Psychology Department. Basing his discussion on memory for what he claims Adams told him many years ago, Klopfer makes a number of inaccurate statements. For example, William McDougall became the Chair of the Duke Psychology Department in the summer of 1927, the same year that Rhine came to Duke, not in the early 1930s as indicated in the text. Rhine received a permanent appointment in Psychology in 1931, the same year that Adams was appointed. Although somewhat negative, Adams initially did not display the animosity to Rhine and his work that he would later. He was even serving as a test subject for Rhine as late as 1936. The thing is that, with less than an hour's research, Klopfer could easily have checked out the details and provided an accurate account -- the information is all there in a book by one of his colleagues in the Duke History Department (Mauskopf & McVaugh, 1980). Given this example, I'd be hesitant to cite historical facts presented in this work without first checking them out in other sources.

All this aside, Klopfer has written a charming book that all animal behaviorists should find both entertaining and thought-provoking. Klopfer's personality shines through the pages; he loves his work and his subjects, and his fellow human beings. He has managed to be both

a productive scientist and a concerned social activist, and to keep his science value-free.

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BOOK REVIEW

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Comparative Psychology: A Handbook, by G. Greenberg and M.M. Haraway (Eds.), New York and London: Garland, 1998.

In the preface, the editors say that, in their version of Comparative Psychology (CP), the central focus is evolution, development, and species-typical behavior. While a broad range of animal species is covered, explicit comparisons are few. I like to think of CP as the study of similarities and differences in psychological mediation, but, in fact, few studies of CP achieve (or even strive to) that desideratum, perhaps the last great work being Razran's (1971) *Mind in Evolution*. Most of us study behavioral differences and similarities, and leave it at that. Even this watered down version of CP (really CB) is found more in the ethological literature than in the literature of CP. And to get one other carp out of the way, this compendium is structured more like an encyclopedia than a handbook, which is intended as a descriptive, not a negative, comment. Namely, the entries are quite brief compared to the chapter-length treatments one encounters in volumes called handbooks.

The text of this book runs to 865 pages and, although I agreed to the first editor's invitation to review this book, I did not read every entry in their entirety. I read the entries that interested me to determine if these entries were accurate, competent, interesting, fairly complete, and usable by students. And many of them were all of these. Thus, I would recommend purchase of the volume for one's laboratory, department, or institutional library.

To see how much of my version of CP there might be, I went to the final section on Cognitive Processes and there discovered a mix of entries on approaches to the study of cognition, cognition in animals (very restricted), counting (careful, concise), honey-bee dance language controversy (makes for spirited reading), language in animals (there is

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also a seemingly never-ending, somewhat depressing controversy here: if nonhuman primates seem to be doing it, is it language as used by humans?), self-recognition in nonhuman primates (what does mirror self-recognition signify?), and tool use (close to the data and alert to pitfalls). All highly analytical and critical – no grand (or even semi-grand) conclusions on comparative psychological mediation, I am afraid.

Next, I went to the Author Index to see how many times my work was cited. One fewer than S. J. Gould, several fewer than the first editor and G. G. Gallup, Jr. As for high counts, Darwin, Lorenz, and Schneirla get four lines each, which seems like justice is being done. (Later I learned that I was cited a bit more than showed up in the Author Index, so I caught up on Gould, provided the same didn't go for him). There is also a Species Index, where humans get almost 12 lines, rats almost 9, and birds 4. There were none for ducks but I know that is wrong as I read about my work in a few places. I also checked mallard duck and wood duck but came up empty (as with their Latin names). Another copyediting glitch is the absence of a List of Contributors with their affiliations to make it a simple matter to contact authors whose topics are of special interest.

The volume begins with a historical and philosophical section, wherein Nancy Innis gives capsule biographical summaries of 29 of the leaders in CP and closely related fields, all but three of whom are deceased (Jeff Bitterman, Nicholas Mackintosh, Ethel Tobach). C.W. Tolman writes a brief Euro-Marxist history of CP. That is succeeded by a nicely crafted review by Jean-Louis Gariépy in which he recounts, in a broadly-based theoretical way, the recent histories of CP, ethology, and the "developmental synthesis," featuring Schneirla and his close colleagues, concluding with the "Modern Developmental Psychobiology," which has carried the theoretical work of Kuo, Schneirla, and Lehrman to its present state, including some extensions to human beings which would have greatly pleased that trio. Section I closes with an international perspective on CP by R. Ardila.

Section II concerns Theory, Concepts, and Issues, topics that will also interest almost all readers. As befits an encyclopedia, here and elsewhere, the order of the entries is determined by the alphabet, so Allometry and Comparative Psychology (Thiessen and Villarreal) leads off with a quite unusual proposal that I was not able to follow but might be read with profit by those interested in "the allometry of behavior," a rarely explored topic (McKinney & Gittleman, 1995). These authors are somewhat ambivalent about the concept of anagenesis, to which they think allometry is complementary, on the one hand, but they reject the idea of evolutionary progress, the kernel of anagenesis, on the other.

Because of the coincidence of the alphabetical ordering, Yarczower's entry on Anagenesis follows, which offers a more detailed understanding of the concept, using Rensch's criteria for identifying instances of anagenesis, and J. Huxley's notion of "grade," as distinct from "clade," which was accepted by leading evolutionists such as Gaylord Simpson and Ernst Mayr. Yarczower's critical discussion of the troublesome concept of evolutionary progress should help to clarify what I and others, following Rensch et al., have tried inadequately to render lucid in other contexts as far as CP is concerned. Other theoretical treatments in this section include Schneirla's A/W Theory (Raines and Greenberg), Developmental Contextualism, lucidly rendered by its author, Richard M. Lerner, Dynamical Systems and Dialectical Processes in Development and Evolution, somehow magically distilled to five pages by Kathryn Hood, Epigenesis, a little too distilled by David B. Miller, and a generous treatment of Evolution by the creative and many-faceted biologist Mae-Wan Ho. I couldn't help but notice a rather garbled account of some of my main experimental findings for which a *field* study is cited (yikes!). Otherwise, Professor Ho coherently presents the latest on non-neoDarwinian accounts of evolution, which she then links to the Schneirla-Lehrman epigenetic critique of Lorenz's theory of the innate and acquired in development. The other two theoretical entries that will seem familiar are Gibsonian Theory in Comparative Psychology (Flynn and Stoffregen) and a balanced evaluation of Sociobiology as a field of study, a theory of social behavior, and a statement about human nature (Moore and Michel). The rest of the section deals with issues such as homology (Burton), individual differences (Mather), instinct (Barnett), behavioral ecology (Klopfer and Podos), motivation (Hogan), species-typical behavior (Haraway and Maples), etc. There is a very arresting entry on Thermodynamics, Evolution, and Behavior (Swenson) to close out this Section, which I believe most readers will find novel but perhaps difficult, although it is concise and well written. It is intended as an optimistic reinterpretation of the second law of thermodynamics (which pictures a world in "degenerative disorder"), calling for self-organizational and autocatakinetic processes to rescue biology and psychology from such a dispiriting state of affairs. The only major item that is missing in Section II is the topic of behavioral heterochrony (Cairns, Gariépy, & Hood, 1990; McKinney & Gittleman, 1995).

Given that – to my way of thinking – a comprehensive theory of comparative psychology will necessarily involve behavioral and psychological anagenesis (e.g., Schneirla's concept of levels in the psychological capacities of animals), it is interesting to note that the entry on Lloyd Morgan's Canon (R.K. Thomas) concludes that the

canon≠parsimony but, rather, Lloyd Morgan's Canon=psychological anagenesis. The problem in its widespread acceptance and application is the lack of a generally agreed upon hierarchy of behavioral and psychological processes. (See, for example, Partridge and Greenberg's entry, Integrative Levels.) Once again, as an exemplar, Razran's (1971) *Mind in Evolution* comes to the fore, in which eleven ascending levels of learning are identified, going from habituation and sensitization at the low end to "symboling (the learning of thinking, planning, and willing)" at the high end. The cerebral underpinning for anagenesis, particularly increases in brain size and cortical evolution, is provided by Jerison's (1973) *Evolution of the Brain and Intelligence*. Anagenesis is further discussed in a cogent way in Hailman's entry, Comparative Methods in Behavioral Studies, in which, by way of contributing to a consensual psychological anagenic scheme (grades of psychological progress), he puts forth the idea that, "If...it could be shown that every animal that can master a reversal discrimination can also learn an oddity problem, but not vice versa, then it could be concluded that the former ability is higher than the latter..." (p.237).

The most intensively comparative of the entries is the entry on Hearing, in which H.E. and R. S. Hefner summarize an enormous literature to which they themselves have made an outstanding contribution. While they conclude "...there is no trend toward better ears," in the review it is possible to tease out anagenic conclusions even in this ecologically highly constrained domain: "Although birds have the best hearing of nonmammalian vertebrates, they do not hear above 12 kHz and their ability to localize sound is generally not as good as that of mammals" (p.295). "In the case of insects, the selective [ecological] pressures have been dealt with in a relatively simple manner: approach a potential mate (or prey) and avoid a predator (bats). Mammals, on the other hand, have evolved the ability to use hearing to respond to sound sources in more sophisticated ways, as illustrated by the communication calls of monkeys and by human language"(p.300).

In the entry on Sleep (W.B.Webb), we learn that all mammals and birds manifest REM (rapid eye movement) and non-REM sleep, whereas there is little or no evidence of REM sleep in reptiles and fish, and the sleep structure in humans (and other primates) is the most complex of all species.

Before leaving the topic of anagenesis, it is necessary to repeat an already oft-repeated caveat: psychological anagenesis represents a nonuniform *trend*; it is not a necessarily universal pattern in the sense that it occurs without exception in all phyla. The concept of comparative psychological anagenesis is the recognition of the emergence of qualitatively progressive novelties in behavioral

characteristics and psychological capacities during the course of evolution. As noted earlier, the term "progressive" causes negative reactions in some comparative psychologists, so let me go on, more concretely, to say the cardinal defining features of comparative psychological anagenesis are increases in developmental psychological adaptability (flexibility) and improvements in behavioral versatility (Gottlieb, 1984). It is not only comparative psychologists who see utility in anagenesis as a separate lineage-transcendent form of evolution. To wit, Hölldobler and Wilson's (1983) noncladistic analysis of "the evolution of communal nest-weaving in ants," in which three progressive "phylogenetic grades" of nest building are discriminated in four independently evolved genera of formicine ants.

It is not possible to do justice to this useful tome in a review of this sort, but I hope I have given enough of the flavor that potential readers will seek it out. I have not touched on all of the eight Sections of the volume—rest assured there is much of interest here for anyone who finds CP, however defined, an attractive field of study. Where else could you learn, except on page 783 of Celia Moore's masterful review of *Vertebrate Sexual Behavior*, that the "Amazon molly, a familiar aquarium fish, is an all-female species that requires sperm from males of a different species to initiate the embryonic development of [its] eggs, although no use is made of the sperm's genetic material"?

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